# Responses of the West European hedgehog to urbanisation: impact on population dynamics, animal movement and habitat selection

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## Copyright statement

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## Contribution statement

Fieldwork and data collection (i.e., camera trapping and spotlight surveys) were carried out by myself in collaboration with several researchers from different institutions:

**Southwell 2016:** myself and Hannah Lockwood (MSc student Nottingham Trent University).

**Reading 2016:** Abigail Gazzard (University of Reading).

**Ipswich West 2017 and East 2018**: Simone Bullion and Alexandra North (Suffolk Wildlife Trust).

**Brighton 2019:** Alexander Audrius Cloke (MSc student Nottingham Trent University) and Dawn M. Scott (University of Brighton).

**Hartpury 2017:** Lucy Bearman-Brown (Hartpury University).

**Sutton Bonington 2018:** myself in collaboration with Tom Reader (University of Nottingham).

Brighton 2018, Brackenhurst 2017 and 2018, Bishop Burton 2019 and Riseholme 2019 were surveyed by myself.

Furthermore, in Chapter 3, Christopher S. Sutherland (University of Massachusetts-Amherst) and Philip J. Baker (University of Reading) helped with the SECR analysis and drafting the manuscript for publication, respectively. The rest of the analysis of Chapter 3 and all the analyses of Chapters 4 & 5 were carried out by myself. I was also responsible for the experimental design with help and guidance from my supervisory team, Dr Richard W. Yarnell, Dr Antonio Uzal and Dr Louise K. Gentle.

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## Abstract

Urbanisation is rapidly increasing, producing drastic changes in the environment. While many species are unable to adapt to these human-made environments, some species not only survive but thrive in urban landscapes. The West European hedgehog *Erinaceus europaeus* is a species of conservation concern in the United Kingdom where populations have declined markedly since the 1950s. Despite declines being reported both in urban and rural areas, the species seems to be persisting in cities and towns. However, current population estimates are unreliable and our understanding of the population status of the species is limited. This study aimed to understand how hedgehogs respond to urbanisation by investigating how their density, movement behaviour and habitat selection varies across urban and rural landscapes.

Between 2016 and 2019, camera trapping and high-frequency GPS movement data were collected across England. Hedgehog densities were calculated from camera trapping data using the Random Encounter Model (REM) across five urban and four rural study sites, and compared to those estimated by Spatially Capture-Recapture using data from nocturnal spotlight surveys. Hedgehog movement was studied across five urban and six rural sites, where home range was evaluated using the Time Local Convex Hull (T-LoCoH) method. Movement behaviour was extracted from GPS data using Hidden Markov Models, incorporated into habitat selection analysis and studied using the integrated step selection analysis.

Hedgehog density, as estimated by the REM, was on average 7.5 times higher in urban versus rural landscapes. The movement of individual hedgehogs differed between both landscapes: urban individuals exhibited slower speeds and travelled shorter distances per night than rural individuals. Nightly home range size was best predicted by sex, landscape and the proportion of gardens used: larger home ranges were displayed by males in the rural landscape, and home range sizes decreased as the proportion of gardens used increased. Hedgehogs spent more time foraging (68%) than travelling (32%) across both landscapes. However, the time spent performing each behaviour varied by sex and landscape. Gardens were found to be important habitats, as they were strongly selected for foraging and travelling behaviours of hedgehogs in both urban and rural areas.

This is the first comparative study to estimate population densities across urban and rural areas in England and provide researchers with a robust methodology that uses camera trapping data and the REM for the monitoring of species. Furthermore, this is the first study to incorporate behaviour extracted from GPS movement data into habitat selection analysis to better understand how hedgehogs are using different habitats in different landscapes. Findings from this study provide important and novel information to aid understanding of how different landscapes are affecting the distribution and behaviour of hedgehogs and how they are exploiting anthropogenic landscape features to persist in cities and towns.

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# CHAPTER ONE

# Introduction and research context

## 1.1 General introduction

Structurally complex habitats can sustain great biodiversity by providing a wide range of resources and niches for different species, influencing animals distribution across the globe (Lawton, 1983; Dean and Connell, 1987; Tews et al., 2004; Kovalenko, Thomaz and Warfe, 2012; Bracewell, Clark and Johnston, 2018). With the Earth's land surface now dominated by human-modified landscapes, global biodiversity patterns and processes have been greatly impacted (McKinney, 2002; Forman, 2009). Although humans have dominated landscapes over the past few centuries, advances in technology during the industrial revolution allowed landscapes to be altered drastically, often causing detriment to biodiversity. For example, over the last century, agricultural intensification in the UK has caused heterogeneous, complex landscapes rich in wildlife to be converted into more homogeneous habitats with reduced habitat quality and lower biodiversity (Robinson and Sutherland, 2002; Fahrig et al., 2011). Conversely, while the anthropogenic impact on the rural landscape has reduced habitat complexity, urban development and expansion have created more complex habitats in cities and towns (Band et al., 2005; Cadenasso, Pickett and Schwarz, 2014). These human settlements range from low housing density areas with extensive green spaces such as parks and gardens, to areas with high building density and limited green spaces (Cadenasso, Pickett and Schwarz, 2014). As a result, characteristics of the urban landscape, such as the availability and distribution of resources, permeability to animal movement, climatic conditions, and levels of light and noise, are also highly variable within cities and towns and, when these factors are combined, they influence which species are able to persist (Gaston, 2010; Parris, 2016). Therefore, the response of wildlife to the urban landscape is highly diverse (Douglas and James, 2014): some species benefit from intermediate levels of urbanisation, e.g., many species of birds (Kettel et al., 2019), while others, such as terrestrial mammals, are less well adapted with the extreme response being that some species are unable to use urban areas (Chace and Walsh, 2006; McKinney, 2008; LaPoint et al., 2015; Parris, 2016).

Urbanisation and densification of cities are expected to continue increasing in tandem with human population growth (McKinney, 2002; Dearborn and Kark, 2010; Ramalho and Hobbs, 2012; United Nations, 2018). By 2030, 60% of the human population will live in urban areas (United Nations, 2018) and, as a result, cities will grow in size and number, i.e., megacities are projected to rise from 33 in 2018 to 43 in 2030 (United Nations, 2018). However, responses of wildlife to urbanisation, and the implication of this in terms of biodiversity in the long-term, are often unknown (Faeth et al., 2005), despite being urgently needed to improve the changes of persistence of species in human-dominated landscapes. Comparative studies of urban and rural populations that allow animal behaviours to be investigated in different landscapes can provide valuable insights for wildlife conservation. Understanding how animals respond to urbanisation, e.g., changes in population densities due to higher carrying capacity, as well as identifying features in the landscape that can help in the long-term persistence of species in the urban landscape, is urgently needed to improve the changes that species will persist. Only then, a better understanding of how wildlife is expected to respond with continuing changes in the environment will help researchers to predict changes in animal behaviour and implement specific conservation management according to the characteristics of different habitats. Such information can be of great value for urban wildlife conservation to inform urban development and make urban environments more suitable for a wider range of species, benefiting biodiversity and the whole urban ecosystem.

### 1.2 Responses of wildlife to urbanisation

Urbanisation alters species composition, usually resulting in a loss of species biodiversity (Douglas and James, 2014). However, urban areas can still sustain a high number of species (Guénard, Cardinal-De Casas and Dunn, 2015; Lepczyk et al., 2017; Wang et al., 2020) and have even been identified as hotspots for some species (Ives et al., 2016). Generalist species are more likely to thrive in human-dominated environments due to their ability to adapt, survive and reproduce in a wide variety of environments by making use of different resources (Forman, 2002; Fryxell, Sinclair and Graeme, 2014; Adams, 2016). Species that are able to adapt to the difficulties found in cities, such as traffic flow, noise and presence of humans, and benefit from the resources available in the urban landscape, are referred to as ‘urban adapters’ (Blair, 1996; McKinney, 2002).

Some of the most common mammal urban adapters are coyotes *Canis latrans*, raccoons *Procyon lotor* and foxes *Vulpes vulpes*. Conversely, 'urban avoiders' are very sensitive to changes in their habitat, so urbanisation causes their populations to decrease and even disappear (Blair, 1996; Rodewald and Gehrt, 2014). Large mammals such as grizzly bears *Ursus arctos horribilis*, bison *Bison bison* and elk *Cervus canadensis* are examples of urban avoiders (McKinney, 2002; Rodewald and Gehrt, 2014). Finally, 'urban exploiters' are species that are dependent on human activities, and reach their highest densities in cities and towns. Examples include cockroaches *Blattodea*, brown rats *Rattus norvegicus* and house mice *Mus musculus* (Blair, 1996; McKinney, 2006). Whether species become adapters, avoiders, or exploiters, relates to how they respond to the drastic physical changes along the urban-rural gradient (Gilbert, 1989).

Phenotypic plasticity, such as the ability of a species to change its behaviour in response to changes in its environment, facilitates species to adjust and persist in the landscape (Ghalambor, Angeloni and Carroll, 2010), whilst further adaptation occurs through genetic change (Evans et al., 2010). Some species are adaptable and can modify their spatial and temporal behaviour patterns to maximise their fitness, which has been reported across a wide range of urban mammals. For example, coyotes increase time spent encamped in highly urbanized areas compared to natural and suburban areas (Ellington and Gehrt, 2019) and hedgehogs *Erinaceus europaeus* increase foraging activity after midnight in residential areas (Dowding et al., 2010) to reduce the risks associated with human activities. In addition, bandicoots *Perameles nasuta* avoid backyards of houses with dogs (Carthey and Banks, 2012); squirrels *Pteromys Volans* move faster and cover longer distances along their movement path in response to increasing amounts of urban habitats (i.e., residential areas, roads) to avoid unsuitable habitats (Mäkeläinen et al., 2016); and hedgehogs (Barthel, 2019) and koalas *Phascolarctos cinereus* (Phillips, 2016) can make short-term changes in their space-use behaviour in response to temporary disturbances such as music festivals. Finally, relaxed territorial behaviours have been reported in urban carnivores such as badgers *Meles meles* (Davison et al., 2009), feral cats *Felis catus* (Mirmovitch, 1995) and mongooses *Mungos mungo* (Gilchrist and Otali, 2002).

### *1.2.1 Population growth rate and density*

For generalist bird and mammal species that are able to persist in a wide range of habitats including urban and rural landscapes, the urban populations tend to exhibit higher growth rates and reach higher densities than conspecifics in rural populations (e.g., Adams, 2016; Kettel et al., 2019). Two main effects have been suggested to explain the higher densities reported in urban areas: a bottom-up effect (i.e. increase in resources availability) and a top-down effect (i.e., decrease in predation; Shochat, 2004; Faeth et al., 2005).

In cities, some species reach population densities that would be unlikely in rural environments. For instance, many medium-sized carnivore 'urban adapters', such as coyotes, red foxes *Vulpes vulpes* and raccoons *Procyon lotor*, reach higher population densities in urban, compared to rural, landscapes presumably due to greater availability of resources (Bateman and Fleming, 2012). Highly concentrated availability of natural (e.g., fruits, insects) and anthropogenic food resources, whether this is intentional, in the form of supplementary feeding, or unintentional, in the form of waste, have been suggested as one of the main reason behind higher densities of urban populations (Bateman and Fleming, 2012). For instance, Fedriani, Fuller and Sauvajot (2001) evaluated local densities of coyotes and anthropogenic food availability across an urbanisation gradient and found that highly urbanized areas not only had the highest coyote density but also a higher percentage of anthropogenic food in the individuals' faeces. In contrast, less urbanized areas had a lower density of individuals, whose diet also had fewer food items from anthropogenic resources (Fedriani, Fuller and Sauvajot, 2001).

The higher availability of natural and anthropogenic food resources can benefit the survival and reproduction of individuals (Brittingham and Temple, 1988; DeNicola et al., 2000; Murray et al., 2016). For instance, female white-tailed deer *Odocoileus virginianus* usually produce one fawn, but twins and triplets can be produced in suburban landscapes if good foraging conditions are available (DeNicola et al., 2000). Supplementary feeding increases the survival rate of black-capped chickadees *Parus atricapillus* by 30% during the winter when higher energetic costs are usually required to access dispersed natural resources (Brittingham and Temple, 1988). However, the excess of food resources is not evenly or randomly distributed but rather clumped in

some areas such as parks, gardens and landfill sites (Adams, 2016). Such distribution of resources forces individuals and species to co-exist in closer proximity to each other than expected (Adams, 2016). Despite higher food availability seeming beneficial for wildlife, such unnatural proximity of individuals can have a negative effect. Indeed, supplementary feeding is associated with high risks of pathogen transmission and increased pathogen accumulation at feeders and in the surrounding environment, potentially resulting in poorer health condition and higher mortality (Murray et al., 2016).

The higher densities of some predator species in urban areas could suggest that predation pressure on prey populations might be greater in urban areas (i.e., predator proliferation; Crooks and Soulé, 1999). However, some behavioural urban studies have reported lower mortality rates and anti-predator behaviours, suggesting that predation pressure is lower in urban areas (Shochat et al., 2006; Valcarcel and Fernández-Juricic, 2009; Stracey, 2011). Such reduction of predation pressure, despite predator numbers being higher, has been referred to as the 'predation paradox' (Shochat, 2004; Fischer et al., 2012), and is recognised as another factor influencing the higher population densities reported in urban landscapes (Shochat, 2004; Faeth et al., 2005). Several non-exclusive mechanisms have been suggested to explain the predation paradox (see Fischer et al., 2012), and food availability again plays an important role (Shochat, 2004). For example, greater food availability promotes hyperabundant prey populations and/or shifts in predator diets to anthropogenic food resources, reducing predation rates on the prey population (Stracey, 2011; Fischer et al., 2012).

### *1.2.2 Animal movement and space use*

Animal movement can play an essential role in the survival of individuals and evolution of species, affecting the dynamics of populations and communities and, ultimately, the function of the whole ecosystem (LaPoint et al., 2015). The movement of individuals is usually associated with goals; animals move to find critical resources such as food and mates and to avoid risks such as predation (Nathan et al., 2008; Holyoak et al., 2008). The movement of animals results in different patterns of space use, which can be studied focusing on the geographic (e.g., home ranges, distribution of species) or on environmental (e.g., habitat use and selection) space (Van Moorter et al., 2016).

Movement and distribution of species are influenced by the availability, quality and spatial and temporal distribution of resources in the landscape (Fretwell and Lucas, 1970; Mitchell and Powell, 2004; McLoughlin et al., 2006; Uboni et al., 2017). For example, in landscapes where resources are clumped, home ranges (i.e., an area that an individual uses over a given period of time for its normal activities excluding occasional excursions; Burt, 1943) are expected to be small, vary little in size and resource content, to be of good quality, and home range overlap should be high and shared by many individuals (Mitchell and Powell, 2004).

In cities and towns, resources are not evenly distributed across the landscape but rather clumped in certain areas (e.g., parks, gardens; Adams, 2016). However, these areas can offer high availability of resources for wildlife (Atwood, Weeks and Gehring, 2004; Prange, Gehrt and Wiggers, 2004; Šálek, Drahníková and Tkadlec, 2015), from naturally occurring (e.g., remnant patches of natural or semi-natural vegetation) to anthropogenic (e.g., garbage, supplementary feeding) food resources which offer rich habitats for urban species (Imhoff et al., 2000; Milesi et al., 2003; Davies et al., 2009; Newsome and van Eeden, 2017). Such distribution of resources in the landscape can influence animal movement (Forman, 2002; McCleery, 2010), reducing the area that individuals need to range to obtain resources (Contesse et al., 2004; Prange, Gehrt and Wiggers, 2004; Davies et al., 2009; Davison et al., 2009). For example, smaller home ranges have been reported in many urban mammal species in comparison to their counterparts in the rural landscape such as red fox, coyote, raccoon, Eurasian badger, white-tailed deer, stone marten *Martes foina*, grey fox *Urocyon cinereoargenteus*, bobcat *Lynx rufus*, striped skunk *Mephitis mephitis*, and woodchuck *Marmota monax* (Gosselink et al., 2003; Atwood, Weeks and Gehring, 2004; Storm et al., 2007; Lehrer and Schooley, 2010; Šálek, Drahníková and Tkadlec, 2015; Ellington and Gehrt, 2019). Higher abundance and clumped distribution of resources can also increase home range overlap and reduce home range size in a wide range of bird species (Robb et al., 2008).

Reduced movement of urban species can also be explained due to movement restrictions caused by habitat fragmentation (Dickman and Doncaster, 1987; Fahrig, 2003; Braaker et al., 2014). For instance, specific features of urban landscapes, such as roads and busy highways, are substantial barriers for the dispersal of coyotes and bobcats (Riley et al., 2006), kangaroos *Macropus giganteus* (Henderson et al., 2018),

salamanders (DeMaynadier and Hunter, 2000) and bumblebees (Bhattacharya, Primack and Gerwein, 2002). Such movement restriction of individuals can reduce gene flow drastically, as shown across different taxa, including the urban fox (Robinson and Marks, 2001; Wandeler et al., 2003), endemic Japanese mouse *Apodemus speciosus* (Hirota et al., 2004), snakes (Dutra et al., 2008) and frogs (Hitchings and Beebee, 1997, 1998; Arruda and Morielle-Versute, 2008), which can lead to lower population persistence (O'Grady et al., 2006).

The quality of the resources also plays an important role in shaping animal movement as it is often assumed that animals prefer good-quality habitats that promote higher fitness (Manly, McDonald and Thomas, 1993; McLoughlin et al., 2006; Uboni et al., 2017). However, the rapid anthropogenic changes in the environment might not provide species with enough time to adapt, generating a mismatch between the environmental cues used to select habitat and the real habitat quality, a behavioural phenomenon known as an 'ecological trap' (Schlaepfer, Runge and Sherman, 2002; Battin, 2004; Hale and Swearer, 2016). Ecological traps can have drastic effects on individual fitness, such as lowering reproductive performance (Hollander et al., 2011), which can lead to local extinctions (Battin, 2004). As 'ecological traps' are expected to increase as drastic changes in the environment continue (Hale and Swearer, 2016), habitat selection studies are needed to understand the importance of different habitats for species and detect unfavourable behaviours that might be detrimental to the persistence of urban wildlife.

## 1.2 Conservation management and research in urban areas

To conserve wildlife effectively in the urban landscape, we need to understand the ecological processes occurring in cities, how individuals are adapting and using different habitats, and what resources such habitats are providing for different species. Only then, can this information be used to inform conservation actions and to implement planning and management across urban landscapes.

### *1.2.1 Urban green space for wildlife*

Green spaces, such as parks, cemeteries, sports fields, golf courses and gardens, comprise an important living component of the urban landscape as opposed to abiotic components such as concrete (Vargas-Hernández, Pallagst and Zdunek-Wielgołaska,

2018). For instance, a study of four British cities (Bristol, Edinburgh, Reading and Leeds) indicated that green spaces represent, on average, 60% of the total landcover within cities (Baldock et al., 2019). Green spaces are beneficial, not only from a social and economic aspect (e.g., increases citizen health and living standards) but also from an ecological perspective, as they soften the impact of anthropogenic activities on the atmosphere (e.g., maintain humidity, moderate temperatures, clean the air), creating sanctuaries for wildlife and enhancing ecological diversity of urban landscapes (Vargas-Hernández, Pallagst and Zdunek-Wielgołaska, 2018; Hunter et al., 2019; Kruize et al., 2019; Singh, Singh and Singh, 2020).

Urban green spaces have been identified as important habitats to promote and maintain biodiversity within cities (Gallo et al., 2017; Parsons et al., 2018a) and to allow movement of organisms (Bolger, Scott and Rotenberry, 2001; Munshi-South, 2012). Green spaces, such as remnant forest patches (i.e., natural habitats that were fragmented and isolated) and man-made habitats including gardens, allotments and playground fields, provide vital resources for wildlife such as food, shelter and nesting sites (Bateman and Fleming, 2012). However, species diversity in urban green spaces is influenced by different factors such as proximity to certain urban features or specific characteristics of the green space available. For example, coyotes and grey foxes show a greater association with green space found in areas with higher building density (Parsons et al., 2018a). The size, habitat composition and connectivity of the green patch are key features that influence species richness of different groups of plants and birds, as larger spaces, with more complex habitats and better connectivity, affect biodiversity positively (Matthies et al., 2017). Furthermore, different types of green space also attract different species (Matthies et al., 2017; Parsons et al., 2018a). For instance, coyote occupancy was high in golf courses and cemeteries but low in city parks, while the opposite was true for opossums (Gallo et al., 2017). Green spaces such as road verges, and patches of remnant forest are also important for dispersing individuals (e.g., Getz et al., 1978; Suckling, 1982; Prevett, 1991; Hämäläinen, Fey and Selonen, 2018).

### *1.2.2 Management of urban green space*

Despite growing evidence of the benefits of green spaces for whole ecosystems (Vargas-Hernández, Pallagst and Zdunek-Wielgołaska, 2018), and the fact that these habitats have long been recognised as an important component in the management of

urban spaces and conservation of urban wildlife (Gilbert, 1989), there is no coordination of management across the globe (Baycan-Levent and Nijkamp, 2009; Yusof and Rakhshandehroo, 2016; Benchimol et al., 2017; Garcia-Garcia et al., 2020), which creates difficulties when comparing and identifying best practices to inform urban development (Baycan-Levent and Nijkamp, 2004, 2009). The availability of urban green spaces across different cities is widely variable (Baycan-Levent and Nijkamp, 2004; Xu et al., 2011; Kabisch et al., 2016; Singh, 2018; Ramaiah and Avtar, 2019; Cobbinah et al., 2021). For example, while green space availably has increased in Western and Southern European cities, it has been reduced in most of the Eastern European cities (Kabisch and Haase, 2013). Due to the positive impact that greening policies can have on increasing the availability of urban green spaces (Kong and Nakagoshi, 2005), and the importance of these habitats for wildlife (Goddard, Dougill and Benton, 2010), urban development should be planned with wildlife in mind (Loram, Warren and Gaston, 2008; Aronson et al., 2014; Gallo et al., 2017), by, for example, promoting good connectivity between urban green areas (Getz et al., 1978; Suckling, 1982; Bennett, 2003; Hämäläinen, Fey and Selonen, 2018) to facilitate movement within the urban landscape (Gallo et al., 2017; Matthies et al., 2017).

Gardens constitute a significant proportion of green space in urban areas, representing 22-36% of total urban land cover (Loram et al., 2007; Baldock et al., 2019), and provide vital ecological functions for wildlife (Goddard, Dougill and Benton, 2010). For instance, gardens with flower beds, bushes, trees and other elements provide shelter and nesting materials for hedgehogs (Braaker et al., 2014), daytime cover for foxes (Harris, 1977), foraging ground for badgers (Cresswell and Harris, 1988), nesting sites for bumblebees (Osborne et al., 2008) and vital habitats for amphibians (Beebee, 1979; Carrier and Beebee, 2003). However, not all gardens are suitable for wildlife. For example, large gardens are more likely to have features such as trees and mature shrubs, creating more complex habitats that wildlife can benefit from (Loram, Warren and Gaston, 2008).

Due to the important role of gardens for wildlife, it is vital to ensure that these habitats are managed with wildlife in mind. Indeed, some institutions are already advocating citizens to take actions into their own hands and manage their property to promote wildlife-friendly areas. For instance, The Royal Society for the Protection of Birds (RSPB)

and The Wildlife Trusts have projects encouraging homeowners to create wildlife-friendly gardens by providing more complex and heterogeneous habitats to create shelter and food for a variety of species over different periods of the year (RSPB, 2020; The Wildlife Trusts, 2020). Also, to promote garden connectivity, the project 'Hedgehog Highway' asks citizens to put holes in their fences to allow movement of hedgehogs through urban areas, as permeable fences have a positive influence on the presence of wildlife in gardens (Hof and Bright, 2009; PTES and BHPS, 2020). Furthermore, the use of hedges along property boundaries is also encouraged, to provide both habitats for wildlife and connectivity between areas (Adams, Van Druff and Luniak, 2005). Initiatives such as these should be increased, as the involvement of citizens in species conservation has several benefits for both citizens and wildlife (Peter, Diekötter and Kremer, 2019).

The management of urban green spaces on large (i.e., city development) and small (e.g., wildlife-friendly gardens) scales is urgently needed to encourage urban wildlife persistence, despite the challenges of living in cities (Ditchkoff, Saalfeld and Gibson, 2006; Aronson et al., 2014). For adequate conservation management of urban landscapes, data about how different features in the landscape affect area requirements of individuals, which features in the landscape promote animal movement, and which habitats provide essential resources, are needed. Furthermore, monitoring the outcomes of management is required to record the efficiency of the actions taken and any changes in the behaviour of individuals or populations as, despite some species adapting to urbanisation, they might not be able to keep up with a constantly changing environment. For example, although bandicoots have exhibited a high degree of resilience to habitat loss and fragmentation in urban landscapes, they are currently under threat as populations are gradually declining, and persistence now depends on the maintenance of patches with high functional connectivity (FitzGibbon, Putland and Goldizen, 2007).

### *1.2.3 Research in urban areas*

Magle et al. (2012) found that most published urban studies focused on animal movement and habitat selection as well as understanding how wildlife responds to urbanisation (i.e., changes in activity levels, foraging behaviour and reproduction output). Although urban wildlife research is a growing field (Adams, 2005; Gehrt, Riley and Cypher, 2010; Werner, 2011; Magle et al., 2012), the number of urban wildlife

studies remain quite low (<2% of overall publications) despite the rate at which cities are developing and impacting biodiversity (Magle et al., 2012).

In order to quantify responses to environmental changes, long-term ecological studies are needed to obtain data related to species, densities and distributions (Lindenmayer et al., 2012; Fryxell, Sinclair and Graeme, 2014). These variables are required to draw conclusions about the status of a community, detect population trends and potential anthropogenic/environmental impacts (Williams, Nichols and Conroy, 2002; Fryxell, Sinclair and Graeme, 2014). Without this information, it is not possible to implement wildlife management strategies or, if already in place, evaluate the responses to those conservation actions.

Surveying urban wildlife is challenging, as observing wildlife from publicly-accessible areas is difficult, and access to private land is usually restricted. Residential gardens are an important component of the urban landscape and provide vital resources for wildlife. However, if researchers were to survey urban areas, contacting a substantial number of urban residents would be required to obtain a representative sample of gardens, as residential gardens cover large areas of the urban landscape altogether, but each garden is usually small (Loram et al., 2007; Davies et al., 2009). Therefore, the cost associated with surveying green urban spaces can be high and logistically challenging. To overcome these limitations, citizen science projects are increasingly being used to monitor urban species (Scott *et al*., 2014, 2018; Hof and Bright, 2016; Croft, Chauvenet and Smith, 2017). These projects rely on collaboration between citizens and researchers, where citizens collect data to answer research questions (Shirk et al., 2012). For instance, Garden BirdWatch has provided 25 years of data on wildlife visiting UK gardens (BTO, 2020), which has allowed a better understanding of urban wildlife communities and behaviour (e.g., Cannon et al., 2005; Chamberlain et al., 2007; Harrison et al., 2010). Due to the advantages that citizen science projects can provide for the research community (Peter, Diekötter and Kremer, 2019), finding suitable methods that could be used by citizens for long-term, large-scale monitoring of wildlife should be explored.

## 1.3 Model species: The West European hedgehog

### *1.3.1 Status and distribution*

West European hedgehogs (*Erinaceus europaeus*) are small, nocturnal, insectivorous mammals that are endemic to Europe, with distributions across urban and rural landscapes in Ireland, Britain and western mainland Europe (Reeve, 1994; Morris, 2006; Amori, 2016). Hedgehogs are currently listed under Schedule 6 of the Wildlife and Countryside Act (WCA) 1981, the Wild Mammals (Protection) Act 1996, the Bern Convention (Appendix III) and classified as Least Concern on the IUCN Red List (Amori, 2016; Morris, 2014). In the UK, the hedgehog is a species of conservation concern and was included in the UK Biodiversity Action Plan 2007 due to its population decline (Battersby and Partnership Tracking Mammals, 2005; Wembridge, 2011; Roos, Johnston and Noble, 2012). The population of hedgehogs was suggested to be 36.5 million in the 1950s (Burton, 1973), with a further decline suggested by Harris et al. (1995) when a population of only 1.555 million in Great Britain was estimated. A more recent study estimated the population of hedgehogs in Great Britain to be 522 000, a further 66% reduction from 1995 (Mathews et al., 2018). Furthermore, a report using citizen science data indicated that between 2000 and 2015, the rural population reduced by at least half, and the urban population by up to a third (PTES and BHPS, 2015). Although the reliability of these estimates is debatable due to sample size (Morris, 2014; Mathews et al., 2018), and the use of different methodologies that do not allow comparisons in the long-term, these studies raised concerns regarding the status of hedgehogs populations in the UK.

The cause of hedgehog decline is thought to be due to a combination of several factors. Across urban and rural areas, a factor affecting hedgehog decline is the increased complexity of road networks which adds to habitat fragmentation, limits landscape connectivity (Rondinini and Doncaster, 2002; Moore et al., 2020), and increases mortality (Wembridge et al., 2016; Moore et al., 2020; Wright et al., 2020). For example, it is estimated that 10-30% of the hedgehog population die on roads (Wembridge et al., 2016). Intraguild competition with badgers can also affect numbers of hedgehogs, either by direct predation or by competition for resources (Doncaster, 1992, 1993; Young, 2005). Indeed, abundance and occupancy of hedgehogs are negatively affected by the presence of badgers, even in habitats regarded as suitable for hedgehogs, such as

gardens and amenity grassland (Young et al., 2006; Yarnell et al., 2014; Williams et al., 2018b).

In rural areas, agriculture has notably changed and intensified in England, transforming the land from one of predominantly mixed farmland to one of a more uniform arable landscape (Robinson and Sutherland, 2002), affecting biodiversity (Donald, Green and Heath, 2001; Vickery et al., 2001; Robinson and Sutherland, 2002). Hedgehogs are usually associated with edge habitats (Hof and Bright, 2010) and feed mainly on macroinvertebrates (Wroot, 1984). Therefore, changes in the complexity of the rural landscape, resulting in the reduction of hedgerows and habitat fragmentation, impact negatively on habitat availability and landscape connectivity for hedgehogs (Yarnell and Pettett, 2020). Moreover, the increased use of pesticides reduces prey availability further (Pelosi et al., 2014).

Despite the overall decline of hedgehogs across their distribution, the species seems to be more abundant in urban areas due to higher food availability and complex landscapes, that provide suitable nesting sites and shelter from predators (Doncaster, 1994; Morris, 2006; Hubert et al., 2011; Pettett et al., 2017b). However, without reliable density estimates and robust comparative studies across urban and rural landscapes that provide long-term population trends, it is not possible to identify the causative factors that are driving the decline of the hedgehog.

One of the reasons for the paucity of density estimates is the difficulty associated with surveying hedgehogs, especially in the urban area where the species seems to be more abundant (Hubert et al., 2011; Doncaster, 1994; Morris, 2006; Pettett et al., 2017b). Population densities of hedgehogs are usually estimated using distance sampling (e.g., Hubert *et al*., 2011) and capture-mark-recapture methods (e.g., Kristiansson, 1990; Jackson and Green, 2000) from visual encounter surveys such as spotlight surveys (e.g., Kristiansson, 1990) and infrared thermographic surveys (e.g., Hubert et al., 2011). Both distance sampling and capture-mark-recapture methods need good sample sizes to produce reliable density estimates (Buckland et al., 1993, 2001; Amstrup, Mcdonald and Manly, 2005; McCrea and Morgan, 2015), and despite that hedgehogs are easily detected in open habitats such as grassland, finding hedgehogs in urban areas can be challenging as the landscape allows individuals to move easily undetected. Furthermore, visual encounter surveys tend to take place along roads, verges and front gardens, which

may be less prefered by hedgehogs (Dowding *et al*., 2010; Rondinini and Doncaster, 2002).

Our current understanding of hedgehog population densities and distributions, and how these vary across habitats and through time, is fundamental for informing future conservation management. Research should, therefore, focus on identifying suitable methods to survey populations of hedgehogs across urban and rural landscapes, that are cost-effective in the long-term and logistically-plausible to implement in urban areas. Ideally, a method that can be implemented as part of citizen science projects to take advantage of the large community currently advocating for the conservation of hedgehogs, is preferred to overcome the limitations of surveying large inaccessible urban areas.

### *1.3.2 Hedgehog ecology*

In the UK, hedgehogs usually hibernate from November to March and are active between April and October, but this varies with the weather (Reeve, 1994; Morris, 2018). Despite both sexes focusing on building fat reserves before and after hibernation, energy allocation of resources during the rest of the active period is highly influenced by sex (Kristiansson, 1984; Rautio, Valtonen and Kunnasranta, 2013; Pettett et al., 2017a). Hedgehogs are largely solitary, with a promiscuous mating system (i.e., both sexes court multiple partners), and parental care is only undertaken by the females (Reeve, 1994; Jackson, 2006; Moran, Turner and O'Reilly, 2009; Morris, 2018). Males often embark on long trips to cover sufficient areas to mate with as many females as possible, while females typically focus their activities on searching for food to meet the high energetic demands of producing and rearing offspring (Fowler, 1981; Barclay, 1989; Du Toit, 2006; Riber, 2006; Dowding et al., 2010; Haigh, O'Riordan and Butler, 2013; Rautio, Valtonen and Kunnasranta, 2013; Rodriguez Recio et al., 2013). This sex-difference in movement and space-use is intensified by the time of the year (Riber, 2006; Dowding et al., 2010; Haigh, O'Riordan and Butler, 2013; Rautio, Valtonen and Kunnasranta, 2013; Rodriguez Recio et al., 2013), with males covering areas up to four times larger during peak breeding activity (Rodriguez Recio et al., 2013).

Another factor that seems to influence the space-use of hedgehogs is the landscape and associated distribution of resources (Riber, 2006; Dowding et al., 2010; Rodriguez Recio et al., 2013; Haigh, O'Riordan and Butler, 2013; Rautio, Valtonen and Kunnasranta, 2013;

Braaker et al., 2014; Pettett et al., 2017b; Rasmussen et al., 2019). However, as most studies focus on either urban or rural landscapes (e.g., Rodriguez Recio et al., 2013; Braaker et al., 2014; Rast, Barthel and Berger, 2019), and different methodologies are usually employed, the insights gained from single-landscape studies may lead to poor inference about space-use patterns across the wider distribution. Nevertheless, rural hedgehogs seem to have larger home ranges than urban individuals (e.g., Riber, 2006; Haigh, O'Riordan and Butler, 2013; Pettett et al., 2017b). Furthermore, green urban spaces, such as gardens, are selected by urban hedgehogs (Dowding et al., 2010), and the features of these habitats seem to influence habitat selection by hedgehogs. For instance, Braaker et al. (2014) found that urban hedgehogs select gardens with structures such as bushes, trees, flower/vegetable beds, stones and branches (Braaker et al., 2014), probably as they can provide shelter, nesting sites and abundant food resources for wildlife (Goddard et al. 2010). Even in the rural landscape, gardens are selected when available (Haigh, O'Riordan and Butler, 2013; Pettett et al., 2017b), although other habitats such as forests and grassland are selected, but to a lesser extent (Riber, 2006; Rodriguez Recio et al., 2013). Despite novel technology, such as GPS tags, being applied increasingly to study hedgehog movement and space-use (e.g., Glasby and Yarnell, 2013; Rodriguez Recio et al., 2013; Braaker et al., 2014; Rast, Barthel and Berger, 2019), research on finer scales is needed to obtain better insights into their habitat use and behaviour in the urban landscape.

### 1.4 Thesis rationale, aims and structure

Due to their wide geographical distribution (Wilson and Reeder, 2005), hedgehogs have been used as a model species to study animal behaviour across a range of habitat types, including urban landscapes (Braaker et al., 2014; Balbi et al., 2019; Barthel, 2019). Urban studies on hedgehogs can help researchers to understand the responses of wildlife to urbanisation and multifaceted pressures of complex urban ecosystems. In addition, they can also highlight potential benefits that towns and cities can provide for wildlife.

This research has found some knowledge gaps that need addressing to benefit research in urban areas, understand responses of mammals to urbanisation, and improve our understanding of hedgehog ecology and conservation. Specifically, the literature is lacking:

1. A suitable methodology that can be implemented to estimate population densities of hedgehogs across different landscapes. Therefore, hedgehog densities in urban and rural areas have yet to be estimated in a comparative manner.
2. Comparable studies of hedgehog home range, as research has been implemented either in urban or rural areas using different methodologies and tracking periods. Therefore, comparison and interpretation of the findings is challenging.
3. Information about hedgehog habitat utilisation in urban and rural areas. Habitat selection studies have highlighted the importance of some habitat types for hedgehogs, however, it is not known how these habitats are being used (e.g., when foraging, travelling, etc).

This thesis is therefore structured so that each data chapter answers one of the knowledge gaps found in the literature:

***Chapter 3: Estimating densities of hedgehogs with camera traps across urban and rural landscapes.*** This chapter implements a novel method that combines camera traps and statistical modelling to calculate and compare the densities of hedgehogs across urban and rural landscapes. This chapter will benefit urban ecology by providing a method that can be used to study and monitor population density trends of urban wildlife. This chapter has been published as an original research article in the peer-reviewed journal *Remote Sensing in Ecology and Conservation* (Schaus et al., 2020).

***Chapter 4: Space-use of hedgehogs in urban and rural landscapes.*** This chapter uses high-frequency GPS data to study space-use by calculating home range size and overlap on consecutive nights, and explores features of the landscape that influence nightly range in urban and rural habitats. This chapter will provide comparable space-use metrics between urban and rural hedgehogs, to better understand space-use across the wider distribution of hedgehogs.

***Chapter 5: Movement behaviour and habitat selection of hedgehogs in urban and rural landscapes.*** This chapter uses high-frequency GPS data to investigate foraging and travelling behaviour of hedgehogs, and to discern habitats selected when displaying these behaviours. This study will provide data about what behaviours hedgehogs are

displaying in different habitat types, and provide better insight into the role of each habitat for the species.

***Chapter 6: General discussion and conclusions.*** This chapter discusses the overall findings of the previous chapters and implications for the conservation of hedgehogs. It highlights the importance of this study to urban wildlife research, and potential avenues for future research.

# CHAPTER TWO

# General methods

## 2.1 Study areas

Five rural and five urban sites were surveyed across England between 2016 and 2019 (Figure 2.1, 2.2 & 2.3). On a national scale, study areas were chosen based on locations where researchers and institutions were interested in surveying hedgehogs (Figure 2.1), while the specific location of the study sites was chosen based on the previous knowledge of hedgehog presence to facilitate the logistics of the fieldwork (Figure 2.3 & 2.3). This approach could have resulted in sampling bias, having most of the rural and urban sites in the midlands and south-eastern areas of England, respectively (Figure 2.1). Despite this potential bias, the final location of the study sites ensured that similar habitats were surveyed within both the urban and rural sites. Furthermore, within each study site, all data collection was carried out as random (e.g., random deployment of camera traps) or exhaustive (i.e., all accessible areas within each study site were surveyed during the spotlight surveys) as possible.

Brackenhurst and Brighton were surveyed twice, on consecutive years, creating a total of twelve study areas. Spatial and temporal dependency was not considered a problem, neither in Chapter 3 as the aim was to compare density estimates provided by two different methods, nor in Chapters 4 & 5 as the sampling unit for all analyses was each individual hedgehog, rather than site. Although I acknowledge that data for three hedgehogs was used for Brackenhurst in consecutive years, this should have not affected the overall results of the analyses.

Populations were assumed closed, as study areas were bound by barriers that should limit hedgehog movements (e.g., major roads; Rondinini and Doncaster, 2002), and surveys were carried out over a short period of time. (Table 2.1).

All data were collected under licence from Natural England (2018-36011-SCI-SCI); ethical approval was granted by Nottingham Trent University's Animal, Rural and Environmental Science Ethical Review Group (code: ARES520).

Land cover of the study areas was mapped using OS Mastermap Topography Layers and high resolution (25cm) Vertical Aerial Imagery (EDINA Digimap Ordnance Survey Service, 2017). Habitat characteristics for each study site were classified as gardens, amenity grassland, arable, pasture, built-up and woodland (Table 2.2). Build-up cover refers to the area covered by buildings, roads and hardstanding (i.e., carparks, driveways).

Landscape types were distinguished according to building density: urban areas were defined as residential towns and cities with more than 20 buildings per ha (Hubert et al., 2011), whereas the remaining sites were classified as rural, consisting of mixtures of arable, pasture, green space and woodland habitats (Table 2.1). As the aim of this study was to investigate hedgehogs across urban and rural landscapes in England, the broad definitions of urban and rural habitats used in this study allowed a differentiation to be made between areas dominated by housing developments (i.e., urban and suburban) and mixed farming (i.e., rural)."

The study area size across rural sites was, on average, larger (76.7 ± 17.5 ha; mean ± SD) than urban (69.2 ± 12.9 ha). The proportion of land covered by amenity grassland was higher in rural (26.3 ± 15.7 %; mean ± SD) than in urban (14.4 ± 7.2 %), while the proportion covered by gardens was much higher in urban (37.6 ± 3.1 %) than in rural sites (1.17 ± 0.9 %). The urban sites also have a larger proportion of their surfaced covered by built-up land (41.8 ± 9.9 %; mean ± SD) than rural sites 14.7 ± 5.7 %).

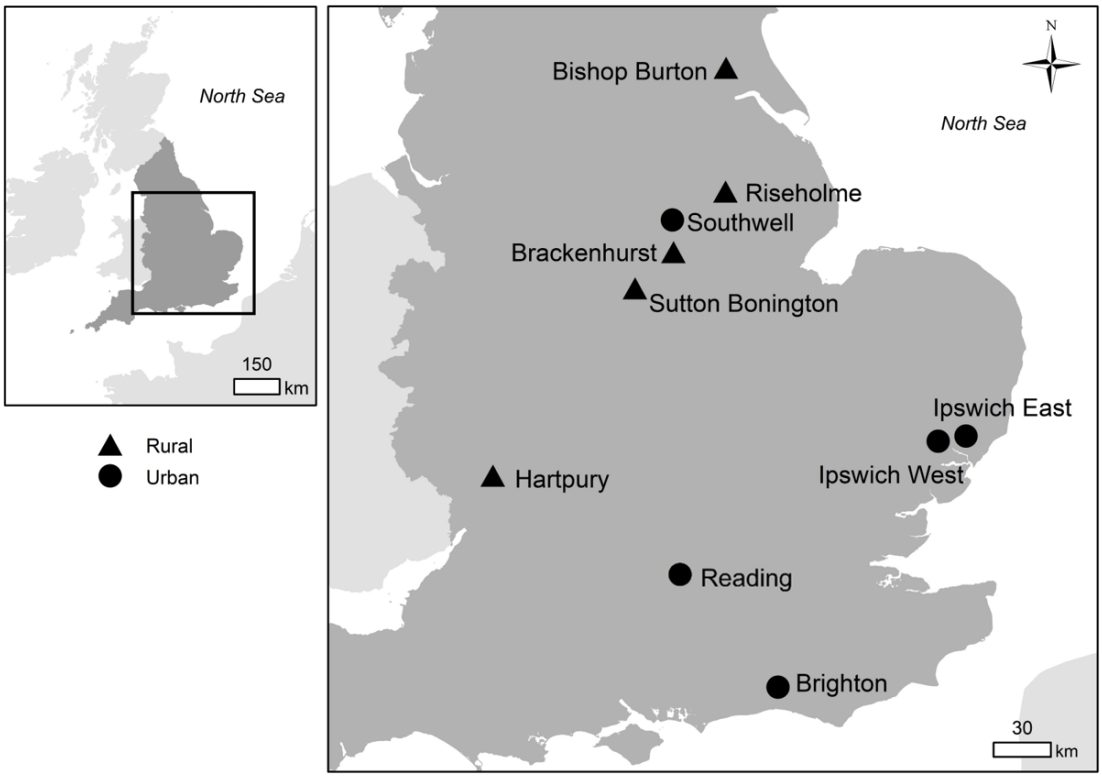
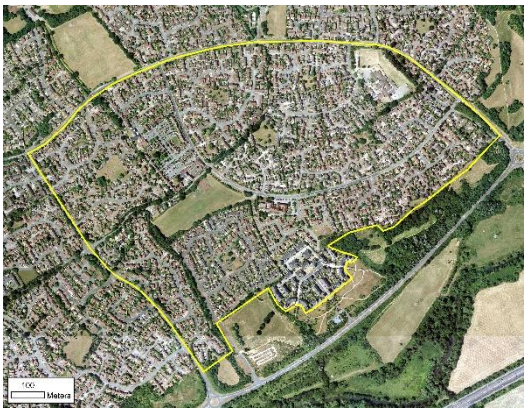



Figure 2. 1 Location of study sites in England, UK. Triangles represent rural study sites (n = 5); circles represent urban study sites (n = 5).

(a) Southwell 2016

(b) Reading 2016



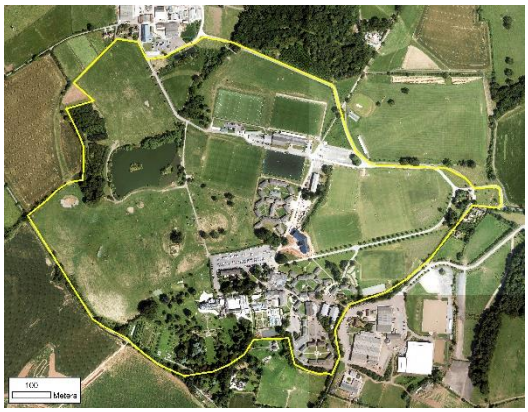
(c) Ipswich 2017

(d) Ipswich 2018

(e) Brighton 2018 /2019

Figure 2. 2 Urban study areas (yellow lines) surveyed between 2016-2019 in England.

(a) Hartpury 2017

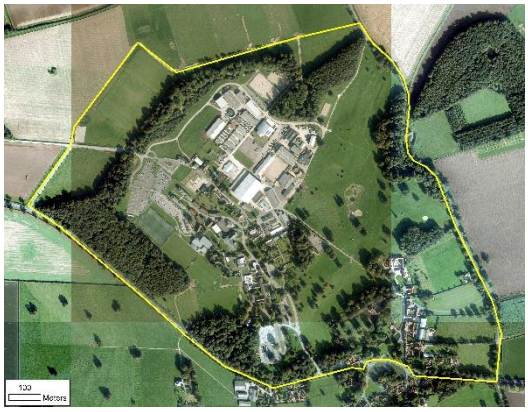


(b) Brackenhurst 2017

(c) Brackenhurst 2018

(d) Sutton Bonington 2018

(e) Bishop Burton 2019



(f) Riseholme 2019

Figure 2. 3 Rural study areas (yellow lines) surveyed between 2016-2019 in England. Despite that Brackenhurst 2017 and 2018 are showing the same aerial image, the landscape of this site was modified between both years but is not reflected in the background images used here. As a result, the study area surveyed at Brackenhurst between both years was slightly modified.

Table 2. 1. Description of urban (n=6) and rural (n=6) independent study sites including survey timing, location (centroid coordinates), study area size (ha), percentage area of each habitat type, and building density (units per hectare). Brackenhurst is listed twice as its habitat composition varied between 2017 and 2018 due to campus development. Brackenhurst and Brighton were surveyed twice on different years. Built-up land refers to the area covered by buildings, roads and hardstanding (i.e., car parks, driveways).

| Landscape | Urban | | | | | | Rural | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site name | Southwell 2016 | Reading 2016 | Ipswich (West) 2017 | Ipswich (East) 2018 | Brighton 2018 | Brighton 2019 | Hartpury 2017 | Brackenhurst 2017 | Brackenhurst 2018 | Sutton Bonington 2018 | Bishop Burton 2019 | Riseholme 2019 |
| Survey period | Jun | Sept-Oct | Apr-May | Apr | May | Jun-Jul | Jun-Jul | Sept | Apr-May | Jul | Aug | Sept |
| Centroid coordinates (Lat/Long) | 53°04'32.40"N 0°57'53.95"W | 51°25'42.50"N 0°54'42.89"W | 52°03'57.88"N 1°07'59.83"E | 52°04'08.52"N 1°11'28.94"E | 50°51'02.45"N 0°12'10.34"W | | 51°54'26.89"N 2°18'34.15"W | 53°03'47.63"N 0°57'22.63"W | | 52°49'53.09"N 1°14'51.55"W | 53°51'03.2"N 0°30'14.8"W | 53°16'07.5"N 0°31'38.9"W |
| Area surveyed (ha) | 67 | 79 | 53 | 85 | 62 | | 63 | 63 | 61 | 77 | 97 | 99 |
| Habitat composition (%) | | | | | | | | | | | | |
| Gardens | 40 | 37 | 33 | 41 | 37 | | 0 | 1 | 1 | 3 | 1 | 1 |
| Amenity grassland | 11 | 11 | 6 | 22 | 22 | | 44 | 10 | 9 | 21 | 44 | 30 |
| Arable | 0 | 0 | 0 | 0 | 0 | | 0 | 0 | 0 | 41 | 3 | 13 |
| Pasture | 1 | 0 | 0 | 0 | 0 | | 28 | 74 | 75 | 13 | 7 | 22 |
| Built-up land | 40 | 47 | 56 | 32 | 34 | | 14 | 12 | 11 | 20 | 23 | 8 |
| Woodland | 7 | 4 | 4 | 4 | 7 | | 10 | 3 | 3 | 1 | 22 | 21 |
| Building density (buildings per ha) | 20.09 | 38.05 | 48.23 | 27.5 | 26.68 | | 1.35 | 5.24 | 4.47 | 3.34 | 2.01 | 1.11 |

Table 2. 2 Landscape and habitats classification and description.

| Category | Classification | Description |
|---|---|---|
| Landscape | Urban | Areas with more than 20 buildings per ha. |
| | Rural | Areas with less than 20 buildings per ha. |
| Habitat | Gardens | Land used for residential and private gardens. No difference was made between front and back gardens. |
| | Amenity grassland | Land covered with grass and used by the general public such as recreational parks, sports fields, road verges, allotments and cemeteries. |
| | Arable | Land used for agriculture. |
| | Pasture | Land covered with grass and other low plants suitable for grazing animals, especially cattle or sheep. |
| | Built-land | Land covered by buildings, roads, carparks, train rails and driveways. |
| | Woodland | Land covered with trees or forest shrubs. |

# CHAPTER THREE

# Estimating densities of hedgehogs with camera traps across urban and rural landscapes

Chapter published as an original research article in the peer-reviewed journal *Remote Sensing in Ecology and Conservation:*

Schaus, J., Uzal, A., Gentle, L.K., Baker, P.J., Bearman-Brown, L., Bullion, S., Gazzard, A., Lockwood, H., North, A., Reader, T., Scott, D.M., Sutherland, C.S. and Yarnell, R.W., 2020. Application of the Random Encounter Model in citizen science projects to monitor animal densities. *Remote Sensing in Ecology and Conservation*, p.rse2.153

## 3.1 Introduction

Information about animal abundance and density, and how these are affected by biotic and/or abiotic factors, are important when developing management strategies and allocating conservation efforts (Fryxell, Sinclair and Graeme, 2014). However, the range of methods available for estimating animal density is substantial (Williams, Nichols and Conroy, 2002), such that it can be a challenge to decide which is best for specific species in different contexts. Ideally, the chosen method should be the one best suited to answering the research question, but factors such as accuracy, precision, cost-effectiveness and appropriateness across different landscapes are often key considerations (Gitzen, Millspaugh and Cooper, 2012; Hayward et al., 2015). Consequently, researchers may produce estimates that are not directly comparable across space or time. This can, in turn, hamper efforts to estimate national and international population sizes which are useful for identifying rates of decline on large spatial scales, and critical to estimating a species' overall conservation status (e.g., Schipper et al., 2008, Croxall et al., 2012; Magera et al., 2013; Mathews et al., 2018).

Finding suitable methods for large-scale, long-term monitoring of abundance is challenging. For example, distance sampling (e.g., Buckland et al., 2001; Giunchi, Gaggini and Baldaccini, 2007; Durant et al., 2011) and capture-recapture methods (e.g., Ruell et al., 2009; Garrote et al., 2011; Lampa et al., 2015;) are often expensive, time-consuming, can be restricted to certain habitats or seasons (Hubert et al., 2011), and may require licenced surveyors if direct capture is necessary (Prange et al., 2014). Furthermore, access to survey sites may be problematic in human-dominated landscapes where

permission is required. This is particularly true in urban areas, such that citizen science projects are increasingly being used to monitor urban wildlife (Scott et al., 2014, 2018; Hof and Bright, 2016; Croft, Chauvenet and Smith, 2017).

One method that circumvents many of the challenges associated with estimating abundance is the use of remote-sensing camera traps (hereafter camera traps). Using cameras to estimate abundance and density from individually identifiable species has been used successfully in a broad range of studies, across many different habitats (see reviews in Burton et al., 2015; Caravaggi et al., 2017), and can involve citizen scientists (e.g., Swanson et al., 2015; McShea et al., 2016). However, estimating densities/abundance is more problematic where individual animals are not distinguishable, e.g., based on pelage or other characteristics. Consequently, Rowcliffe et al. (2008) proposed the Random Encounter Model (REM) whereby population density is estimated by modelling the rates of contact between animals and camera traps, without the need for individual recognition. To date, the REM has only been used to study a limited range of species and habitats (e.g., Rowcliffe et al., 2008; Rovero and Marshall, 2009; Manzo et al., 2012; Zero et al., 2013; Rahman, Gonzalez and Aulagnier, 2017) and while its correspondence with spatial capture-recapture (SCR) methods has not been widely evaluated, Anile et al. (2014) found that camera trapping data analysed with SCR and REM methods produced overlapping population estimates of European wildcat *Felis silvestris*.

As with other camera trapping approaches, the REM has constraints, including purchase costs, theft of equipment, and differences in the reliability and detection performance of different makes and models of the camera (Burton et al., 2015; Caravaggi et al., 2017). In addition, one potentially significant obstacle for the inclusion of citizen surveyors in REM studies is the need for accurate measurements to be taken from photo/video recordings at each location where the focal species has been detected, as inaccurate measurements of the speed of movement and camera detection area could markedly affect estimates of animal density. One way around this problem is to conduct pilot studies, whereby researchers collect data in a representative sample of habitats using a standardised approach (e.g., using the same camera type). Mean estimates of key parameters can then be derived and applied to more substantive studies which still

involve citizen surveyors but negate the pitfalls associated with inexperienced data collectors.

The aim of this study is to assess the effectiveness of the REM for estimating the density of West European hedgehogs (*Erinaceus europaeus*) across urban and rural landscapes in England. This species is currently of conservation concern (Joint Nature Conservation Committee, 2010) as populations have declined markedly since the 1950s (Wembridge, 2011; Roos, Johnston and Noble, 2012) in both rural and urban environments (Wembridge, 2011; Yarnell et al., 2014; Williams et al., 2018a; b). However, there is a paucity of information about hedgehog densities in different habitats because of the lack of a suitable method for estimating density on both small and large spatial scales. Specifically, we: (1) compare hedgehog densities using the REM, based upon site-specific versus averaged parameter estimates; (2) compare density estimates derived from the REM to those generated using Spatial Capture-Recapture (SCR) methods, applied to nocturnal spotlight counts; and (3) test the suitability of the REM for large-scale, long-term species monitoring, based on cost and power to detect population changes. These findings are discussed in the context of the REM's suitability for the long-term monitoring of unmarked individuals across different landscapes, involving citizen surveyors.

## 3.2 Methods

Three rural and five urban sites across England were surveyed between 2016 and 2018 (Figure 2.1; Table 2.1). Brackenhurst was surveyed in both 2017 and 2018, but these were considered temporally independent (e.g., Tinker et al. 2017), creating a total of nine density surveys.

### *3.2.1 Camera trapping*

Following Rowcliffe et al.'s (2008) suggestions for required survey effort based on expected animal density (Hubert et al., 2011) and daily movement range (Dowding et al., 2010), 120 camera trap locations (CTLs) were randomly generated for each study site using Geospatial Modelling Environment (GME) (Version 0.7.4.0; Beyer, 2015). Thirty cameras (Bushnell 119537 Trophy Cam 8MP Night Vision; Bushnell Outdoor Products, Overland Park, KS, USA) were deployed within each study site simultaneously and moved to new locations four times; each camera remained in one location for at least 5

consecutive nights (mean = 6.2 ± 0.04 SE) before being moved. To ensure an even distribution of cameras across each study area, the minimum spacing between cameras was calculated using the inverse of the square root of the number of camera positions per week (30), divided by the size of each study area (Bartolommei, Manzo and Cozzolino, 2012; Balestrieri et al., 2016).

Community engagement took place to obtain permission to place camera traps in urban gardens, targeting the houses closest to the randomly-generated CTLs. Where the householder did not grant permission, the next nearest garden to the random point was targeted until permission was obtained. When random points were located on roads or inaccessible areas, they were moved to the closest garden. Access to rural sites was obtained by contacting the landowners.

Unbaited cameras were attached to posts, fences, wooden stakes, or trees, approximately 0.2m above the ground so that passing hedgehogs would be detected. In urban areas, cameras were placed in back gardens, enclosed front gardens, school grounds, or in discreet locations in recreational parks to reduce the chances of theft. Cameras were set to work on night mode (dusk till dawn), and to record 30-second video clips with a one-minute interval between each. The one-minute delay was chosen to provide a balance between punctuated sampling and continuous monitoring, minimising the risks of missing independent detections whilst reducing battery wastage through multiple recordings of the same individual (Henschel and Ray, 2003; Rowcliffe et al., 2008). *All* other functions *were* left on the *default settings*. Some householders indicated that they regularly placed supplementary food in their gardens; these houses (Brighton, n = 4; Ipswich 2017, n = 1; Ipswich 2018, n = 2) were included in the analyses as they represented the *a priori* availability of food that the hedgehogs would likely encounter. Conversely, if evidence was found that food was provided as a consequence of involvement in the study, these data (Reading, n = 3; Ipswich 2017, n = 3) were excluded to avoid violating the assumption of independent movement in relation to the cameras (Rowcliffe et al. 2008).

Camera-trapping rates were converted to density estimates (D; individuals $km^{-2}$) using independent videos only (Rowcliffe et al. 2008). Specifically, density (D) was estimated as:

$$D = \frac{y}{t}\frac{\pi}{vr(2+\theta)}$$

where $y$ = number of detections of the focal species, $t$ = survey effort, $v$ = daily movement range, and $r$ and θ are the radius and arc of the camera trap detection zone, respectively (see Rowcliffe et al., 2008). Survey effort (t, hours) was calculated as the number of trapping nights per site multiplied by the number of hours the cameras were active per night; the latter was calculated as the period between the earliest and latest hedgehog recording on that site. When a camera was moved or turned off by homeowners, knocked down by livestock, ran out of battery, or if memory cards or cameras malfunctioned, survey effort was reduced by subtracting the total number of affected hours. Camera detection parameters were obtained for each video on-site when the cameras were collected; by playing the videos on a laptop, surveyors were able to use landmarks (e.g., buildings, trees, edges, rocks) as reference points to determine the exact location of the hedgehog with respect to the camera, and to take measurements of the detection arc (θ, radians) and distance ($r$, metres) using a compass and tape measure.

Animal speed was also extracted from videos to calculate the daily movement range ($v$, km $h^{-1}$). This was calculated by multiplying the travel speed ($\mu$) by the proportion of time spent active ($p$), where travel speed ($\mu$) was determined by dividing the distance travelled while in the detection zone by the time the animal was seen on the video (Rowcliffe et al., 2016). The proportion of time spent active ($p$) and its variance was obtained using the R package *activity* (Rowcliffe et al., 2014).

Ideally, to avoid bias, the REM parameters should be obtained for each specific survey (Rowcliffe et al., 2008), but obtaining these data is difficult and time-consuming. Therefore, we compared REM density estimates for each site based on site-specific parameters and mean parameter estimates averaged across sites (Pfeffer et al., 2017; Rahman, Gonzalez and Aulagnier, 2017). This would be amenable for use in a large-scale programme involving citizen science surveyors, as the surveyors would only be required to collate data on detection, rather than the additional effort required for distance and speed parameters for each detection event. Survey effort was calculated independently for each site. Variance and 95% confidence limits were estimated by non-parametric

bootstrapping (Rowcliffe et al., 2008). All analyses were performed in R 3.2.2 (R Core Team, 2017) using the package *remBoot* (Caravaggi et al., 2016).

### *3.2.2 Spotlight surveys and Spatial Capture-Recapture models*

As the true densities of hedgehogs at each site were unknown, reference densities were calculated by analysing individual encounter history data from nocturnal spotlight surveys using spatial capture-recapture models (SCR; Efford, 2004). SCR is an extension of traditional (non-spatial) capture-recapture that estimates population density from spatially-referenced detections by incorporating information such as movement, the spatial organisation of detectors, and space use by individuals (Royle, Fuller and Sutherland, 2018). Hedgehogs were surveyed at night along pre-defined transects across publicly-accessible land (Dowding et al., 2010). For each site, the pre-defined transect was surveyed with uniform intensity on each night. Survey effort varied from 6-20 nights per site. All hedgehogs found during the spotlight surveys were approached on foot and captured by hand, weighed (g) using an electronic balance (Salter 1035 platform scale) and sexed (Morris, 2006). Animals were classified as adults if they weighed >600g (Young et al., 2006; Haigh 2011; Hubert et al., 2011). Healthy adult hedgehogs were uniquely marked with five coloured heat-shrink tubes (10mm in length) on different positions on the hedgehogs dorsal surface. The combination of different colours and locations of the tubes provided an unique mark to allow the identification of each individual. Tubes were attached to the doral spines using a portable soldering iron. Hedgehogs were classed as being 'healthy' if they had few (<5) visible external parasites (ticks), no injuries and normal ball-curling anti-predator behaviour. No hedgehog was marked unless compliant with these criteria. All hedgehogs were released at the point of capture and were observed from a distance until they moved off. The locations of all individuals were recorded using a handheld GPS device (Garmin GPS 60).

For analysis, each transect was divided into 50m 'trap' sections to ensure that the effective trap size was small enough in relation to the home range of the hedgehogs to allow detection in multiple traps, but also large enough for computational tractability relative to a continuous space model (Sutherland et al., 2018). To create spatial encounter histories, the location of each hedgehog's capture/recaptures was transposed to the midpoint of the closest 'trap' and to a sampling occasion (defined as

the whole study area being surveyed). Data from two consecutive sampling nights were pooled if the whole study area was not surveyed on a single night. Location manipulations were performed in ArcGIS 10.3.1 (ESRI, 2015); only adult individuals were included in the analysis, and as such, densities reported relate to adult densities.

In total, eight SCR models were fitted: the null model (no covariates) and all additive combinations of constant and session-specific density (D), sex-specific detection (p) and sex-specific space use (σ). Models were ranked according to the Akaike's Information Criterion (AIC) value (Burnham and Anderson, 2004) and fitted in R (R Core Team, 2017) using the package oSCR (version 0.42.0; Sutherland, Royle and Linden, 2016).

Bland-Altman plots were used to compare densities estimated by the averaged REM and the most parsimonious SCR model (Bland and Altman, 1999; Giavarina, 2015) at each site. The Bland-Altman plot is a method for quantifying the difference between two quantitative measurements by calculating the difference for each pair of values, plotting these differences against the corresponding means, and constructing limits of agreement. Limits of agreement were calculated from the mean $(\bar{d})$ and standard deviation ($s$) of the differences. We expected 95% of the differences to lie between $\bar{d} \pm 1.96s$. All figures cited in the Results are mean ± SE unless stated otherwise.

### *3.2.3 Future population monitoring using REM*

The suitability of the REM for long-term monitoring was assessed based on its power to detect 10%, 25% and 50% changes in population density with a statistical power of 0.80, 0.95 and 0.99, and on the sample size (number of CTLs) required in future surveys. Power (defined as 1-β, where β is the probability of a Type II error: Steidl, Hayes and Schauber, 1997) was calculated using two-tailed paired-sample *t*-tests. Analyses were implemented in the R package *pwr* (version 1.2-2; Champely, 2018).

The costs associated with the REM were estimated from start-up costs (equipment purchases), human resources and survey length (number of days from recruiting volunteers to the collection of the last camera traps) for urban and rural landscapes separately. Although only 30 cameras were used each week, equipment costs were calculated for the purchase of 40 cameras to account for damage and malfunction. Human resources were quantified in terms of the hours of labour required to conduct the survey, including community engagement, fieldwork (i.e., deployment/collection of

cameras, measurements of parameters) and data analyses, although hours of labour were not available for two study areas (Hartpury and Reading). Labour costs were calculated using the 2018 minimum national UK wage of £7.83/hour as a minimum salary benchmark.

### 3.3 Results

Hedgehogs were detected by camera trapping and spotlight surveys at all sites. However, the REM could not be implemented at one site (Sutton Bonington) due to the small sample size (only one camera recorded hedgehogs). Camera trapping surveys were associated with a trapping effort of 47,507 hours and 802 independent hedgehog videos (Table 3.1). Video clips of other species recorded included domestic cats *Felis catus* (n = 1058), foxes *Vulpes vulpes* (n = 550), rabbits *Oryctolagus cunniculus* (n = 549) and badgers *Meles meles* (n = 44). Spotlight surveys were associated with a trapping effort of 613 hours over 1,415 km of walked transects; 111 individual hedgehogs were captured, of which 45 (41%) were recaptured (Table 3.2).

There was a high degree of concordance in REM-derived density estimates derived from site-specific parameters and those derived from averaged parameters (Figure 3.1). The greatest disparity was evident in Reading, with densities being much higher when estimated using site-specific information. Hedgehog densities were higher within urban (averaged REM = 32.3 $km^{-2}$) versus rural (4.3 $km^{-2}$) areas. Mean camera detection arc (θ) and distance (*r*) were 0.245 ± 0.038 radians and 1.97 ± 0.44 metres, respectively. The mean daily movement range was 0.52 ± 0.14 km $h^{-1}$(Table 3.3).

The most parsimonious SCR model (i.e., simplest model with good explanatory predictive power with as few predictor variables as possible; Crawley, 2012) included the combination of session-specific density (D), constant detection (p) and sex-specific space use (σ) (Table 3.4). As with the averaged REM, hedgehog densities derived using the SCR method were higher in urban versus rural locations (Figure 3.1; Table 3.5). Densities estimated by the averaged REM and SCR models were comparable for each site, with both methods producing estimates with overlapping 95% CIs (Figure 3.1). In addition, the mean differences of the densities estimated by the two methods were within the limits of agreement at eight sites (Figure 3.2). However, the averaged REM was more precise than the SCR at seven out of the eight sites; the exception was Ipswich 2017, where a very high density with an extremely large 95% CI was estimated by the

averaged REM in relation to both the corresponding SCR estimate for that site, but also to all other urban sites.

Table 3. 1. Summary of camera trapping surveys.

| Landscape | Urban | | | | | Rural | | | | TOTAL |
|---|---|---|---|---|---|---|---|---|---|---|
| Study site | Southwell 2016 | Reading 2016 | Ipswich 2017 | Ipswich 2018 | Brighton 2018 | Hartpury 2017 | Brackenhurst 2017 | Brackenhurst 2018 | Sutton Bonington 2018 | |
| No. trap nights | 746 | 632 | 711 | 774 | 708 | 660 | 723 | 308 | 754 | 6016 |
| Trapping effort (hours) | 5222 | 6952 | 5688 | 5418 | 4956 | 3960 | 6507 | 2772 | 6032 | 47,507 |
| No. working CTLs | 112 | 120 | 118 | 118 | 109 | 120 | 117 | 59 | 101 | 974 |
| No. CTLs with footage | 74 | 59 | 108 | 75 | 78 | 75 | 26 | 22 | 34 | 551 |
| % of CTLs with footage of hedgehogs | 32% | 23% | 56% | 24% | 14% | 13% | 9% | 7% | 1% | 21% |
| No. videos of hedgehogs | 110 | 89 | 409 | 77 | 56 | 22 | 21 | 12 | 6 | 802 |

Table 3. 2. Summary of nocturnal spotlight surveys.

| Landscape | Urban | | | | | Rural | | | | TOTAL |
|---|---|---|---|---|---|---|---|---|---|---|
| Study site | Southwell 2016 | Reading 2016 | Ipswich 2017 | Ipswich 2018 | Brighton 2018 | Hartpury 2017 | Brackenhurst 2017 | Brackenhurst 2018 | Sutton Bonington 2018 | |
| No. survey sessions | 11 | 8 | 6 | 15 | 10 | 10 | 13 | 17 | 20 | 90 |
| Survey effort (hours) | 40 | 42 | 42 | 124 | 37 | 59 | 27 | 40 | 202 | 613 |
| Total km walked | 141 | 110 | 88 | 372 | 116 | 169 | 88 | 111 | 220 | 1,415 |
| No. hedgehogs captured | 20 | 16 | 14 | 19 | 19 | 8 | 5 | 8 | 2 | 111 |
| % of hedgehogs recaptured | 35% | 6% | 29% | 21% | 58% | 63% | 80% | 100% | 50% | 41% |

Table 3. 3. REM parameters obtained at each site, and the average across all sites. These were used to obtain site-specific (ssREM) and average (aveREM) densities. SD= Standard Deviation.

| Landscape | Urban | | | | | Rural | | | Mean | SD |
|---|---|---|---|---|---|---|---|---|---|---|
| Study site | Southwell 2016 | Reading 2016 | Ipswich 2017 | Ipswich 2018 | Brighton 2018 | Hartpury 2017 | Brackenhurst 2017 | Brackenhurst 2018 | | |
| Average speed ( μ, km/h) | 0.77 | 0.40 | 0.55 | 0.52 | 0.64 | 1.04 | 0.50 | 0.74 | 0.65 | 0.20 |
| Activity level (p) | 0.83 | 0.73 | 0.79 | 0.84 | 0.75 | 0.61 | 1.05 | 1.00 | 0.83 | 0.14 |
| Daily movement range (v, km/h) | 0.64 | 0.29 | 0.43 | 0.44 | 0.48 | 0.63 | 0.53 | 0.74 | 0.52 | 0.14 |
| Detection distance (r, m) | 1.81 | 2.01 | 2.59 | 1.53 | 2.23 | 2.53 | 1.56 | 1.50 | 1.97 | 0.44 |
| Detection arc (ɵ, radians) | 0.244 | 0.209 | 0.209 | 0.262 | 0.262 | 0.314 | 0.209 | 0.209 | 0.240 | 0.038 |

*Sutton Bonington 2018 was not included in the average as only 1 camera recorded 6 videos
(Sutton Bonington parameters: μ=0.18, p=1.29, v=0.23, r=112, ɵ= 0.279)

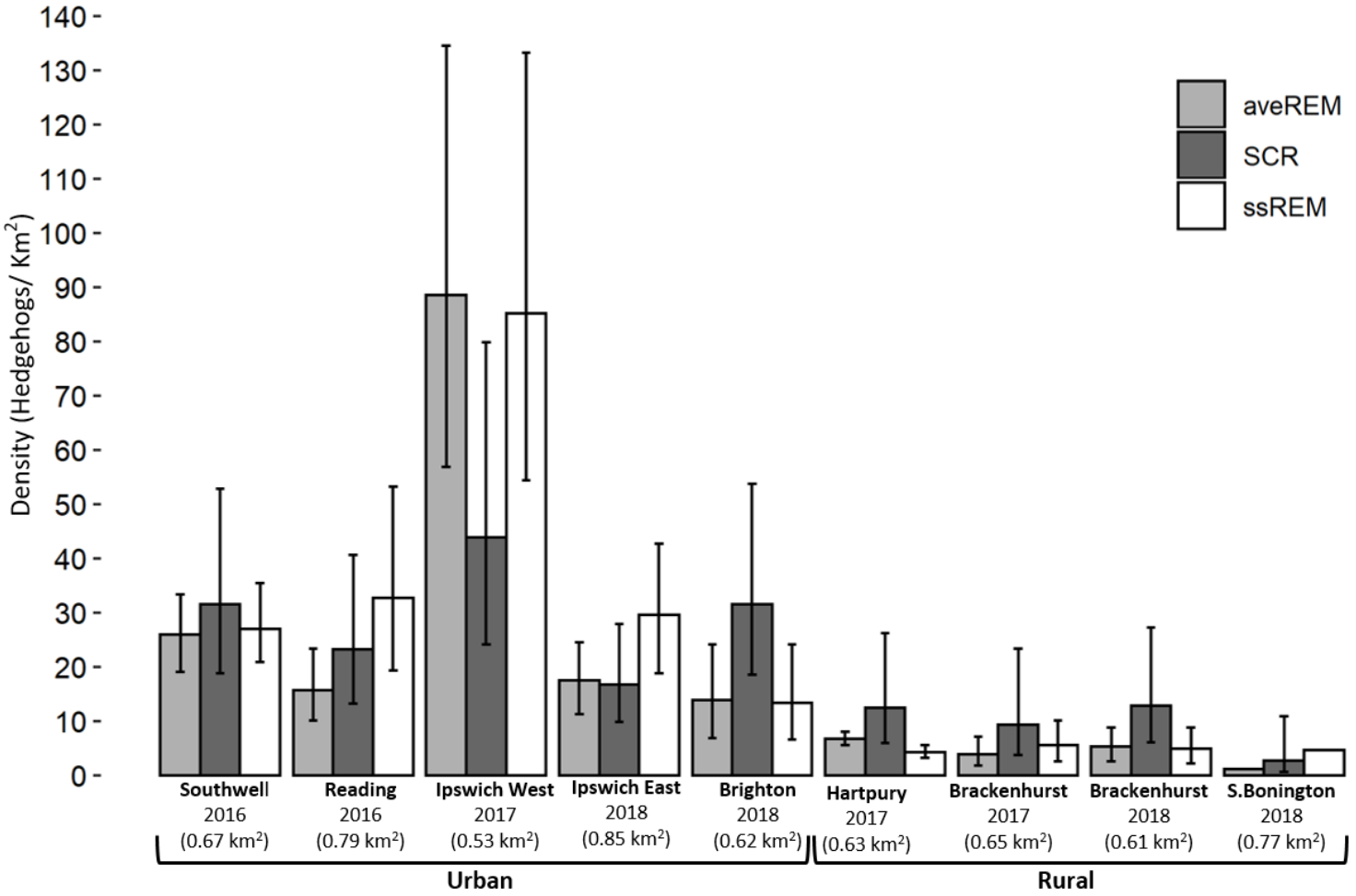



Figure 3. 1 Hedgehog density ($km^{-2}$) estimates derived from averaged Random Encounter Model parameters (aveREM), site-specific Random Encounter Model parameters (ssREM), and Spatial Capture-Recapture (SCR) methods in urban (n = 5) and rural (n = 4) environments. Error bars represent 95% confidence intervals.

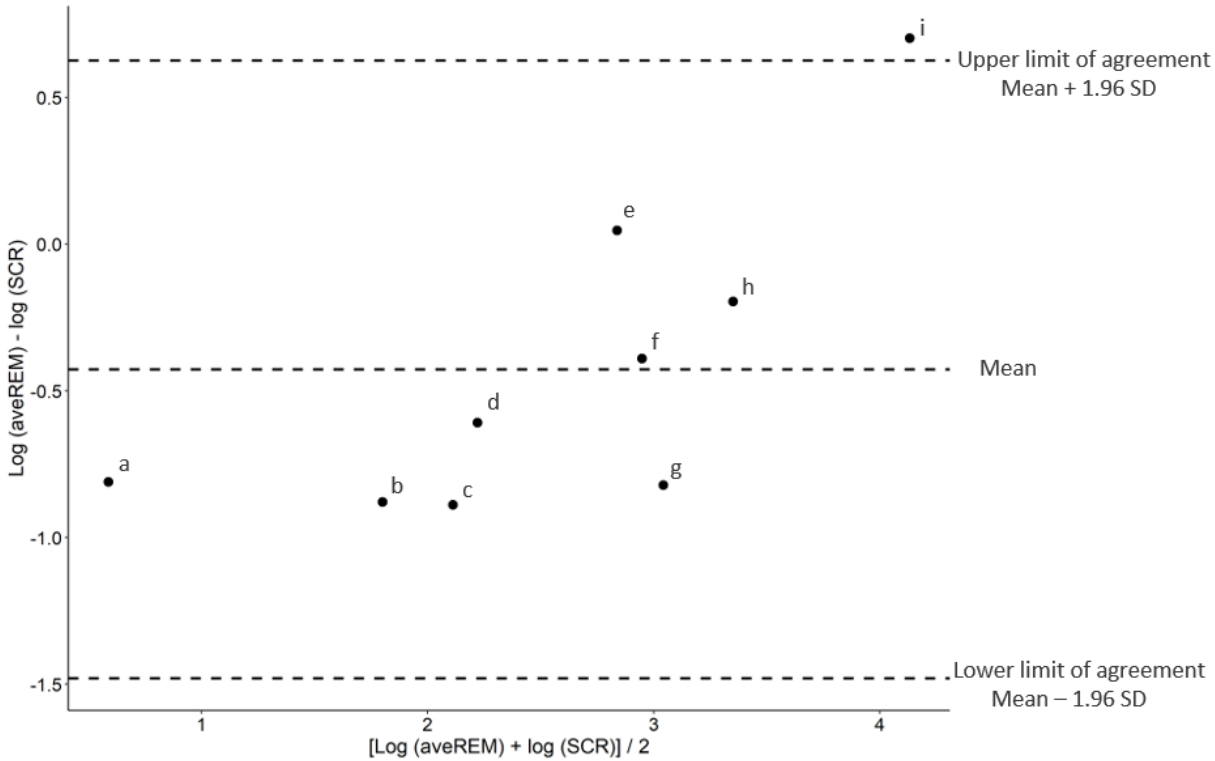



Figure 3. 2 Bland-Altman plot of log-transformed difference [aveREM -SCR] against log-transformed mean density [(SCR+REM)/2] and limits of agreement between the SCR and averaged REM estimates of hedgehog density ($km^{-2}$) at each site: (a) Sutton Bonington, (b) Brackenhurst 2017, (c) Brackenhurst 2018, (d) Hartpury, (e) Ipswich East, (f) Reading, (g) Brighton, (h) Southwell and (i) Ipswich West. The dashed lines represent the log-transformed upper and lower 95% CI of agreement limits.

Table 3. 4. Spatial Capture-Recapture candidate models and specific coefficients values used to estimate densities of hedgehogs in urban and rural landscapes. K= number of parameters, AIC= Akaike's Information Criterion, $\Delta_i$ = delta AIC, $\omega$ = AIC weighting, Cum $\omega$ = cumulative weighting.

| Model | K | AIC | $\Delta_i$ | $\omega$ | Cum $\omega$ |
|---|---|---|---|---|---|
| D(~session) p(~1) sig(~sex) | 13 | 2625 | 0.00 | 0.46 | 0.46 |
| D(~session) p(~sex) sig(~sex) | 14 | 2625 | 0.51 | 0.36 | 0.82 |
| D(~session) p(~1) sig(~1) | 12 | 2627 | 2.57 | 0.13 | 0.95 |
| D(~session) p(~sex) sig(~1) | 13 | 2629 | 4.34 | 0.05 | 1.00 |
| D(~1) p(~1) sig(~sex) | 5 | 2648 | 23.60 | 0.00 | 1.00 |
| D(~1) p(~sex) sig(~sex) | 6 | 2649 | 24.06 | 0.00 | 1.00 |
| D(~1) p(~1) sig(~1) | 4 | 2651 | 26.15 | 0.00 | 1.00 |
| D(~1) p(~sex) sig(~1) | 5 | 2653 | 27.92 | 0.00 | 1.00 |

Table 3. 5. Hedgehog density (individuals per $km^{-2}$) at urban and rural sites estimated using the averaged Random Encounter Model parameters (aveREM), site-specific Random Encounter Model parameters (ssREM), and Spatial Capture-Recapture (SCR) method. Figures in parentheses are 95% confidence intervals.

| Landscape | Urban | | | | | Rural | | | |
|---|---|---|---|---|---|---|---|---|---|
| Study site | Southwell 2016 | Reading 2016 | Ipswich 2017 | Ipswich 2018 | Brighton 2018 | Hartpury 2017 | Brackenhurst 2017 | Brackenhurst 2018 | Sutton Bonington 2018 |
| aveREM density estimate (95% CI) | 25.9 (19.1-33.3) | 15.7 (10.1-23.3) | 88.6 (56.9-134.5) | 17.5 (11.3-24.5) | 13.9 (6.9-24.1) | 6.8 (5.6-8.1) | 3.9 (1.8-7.1) | 5.3 (2.6-8.8) | 1.2 * |
| ssREM density estimate (95% CI) | 27.0 (20.9-35.5) | 32.7 (19.4-53.2) | 85.2 (54.4-133.3) | 29.6 (18.8-42.7) | 13.4 (6.6-24.1) | 4.3 (3.2-5.6) | 5.6 (2.6-10.1) | 4.9 (2.2-8.8) | 4.7 * |
| SCR density estimate (95% CI) | 31.5 (18.8-52.9) | 23.2 (13.2-40.6) | 43.9 (24.1-79.9) | 16.7 (9.9-27.9) | 31.6 (18.6-53.7) | 12.5 (5.9-26.2) | 9.4 3.7-23.4) | 12.9 (6.1-27.2) | 2.7 (0.7-10.9) |

*not enough data available to estimate 95% CI

### *3.3.1 Power analyses*

Using a paired approach, all surveys conducted in this study would have been able to detect a 25% change in hedgehog density with >90% power (Table 3.6). Therefore, following our study design of deploying cameras for 6 nights (± 0.04) in an area of 0.68km$^2$ (± 0.03), 51 and 34 CTLs would be needed in rural and urban areas, respectively, to detect a 25% change in population density with 90% power (Table 3.7).

Table 3. 6. The statistical power of the averaged Random Encounter Model to detect 10%, 25% and 50% of population change between two surveys. Sample size refers to the number of camera trap locations at each site.

| Landscape | Study site | Sample size | Power to detect the stated change in density | | |
|---|---|---|---|---|---|
| | | | 10% | 25% | 50% |
| Urban | Southwell 2016 | 110 | 0.99 | 1 | 1 |
| | Reading 2016 | 120 | 0.97 | 1 | 1 |
| | Ipswich 2017 | 115 | 0.90 | 1 | 1 |
| | Ipswich 2018 | 118 | 0.98 | 1 | 1 |
| | Brighton 2018 | 109 | 0.66 | 0.99 | 1 |
| Rural | Hartpury 2017 | 120 | 1 | 1 | 1 |
| | Brackenhurst 2017 | 117 | 0.51 | 0.99 | 1 |
| | Brackenhurst 2018 | 59 | 0.43 | 0.99 | 1 |

Table 3. 7. Number of camera trap locations (CTLs) needed to detect 10%, 25% and 50% population change with 0.80, 0.90 and 0.95 statistical power in future surveys. Sites arranged by the coefficient of variation (CV) values.

| Study site | Hedgehog density ($km^{-2}$) | CV (%) | % change in density | No of CTLs required to achieve stated level of statistical power | | |
|---|---|---|---|---|---|---|
| | | | | 0.80 | 0.90 | 0.95 |
| Hartpury 2017 | 6.8 | 9 | 10 | 14 | 18 | 22 |
| | | | 25 | 4 | 4 | 5 |
| | | | 50 | 2 | 3 | 3 |
| Southwell 2016 | 25.9 | 14 | 10 | 34 | 44 | 55 |
| | | | 25 | 7 | 8 | 10 |
| | | | 50 | 3 | 4 | 4 |
| Ipswich 2018 | 17.5 | 19 | 10 | 61 | 81 | 100 |
| | | | 25 | 11 | 14 | 17 |
| | | | 50 | 4 | 5 | 6 |
| Reading 2016 | 15.7 | 20 | 10 | 67 | 89 | 109 |
| | | | 25 | 12 | 15 | 19 |
| | | | 50 | 4 | 5 | 6 |
| Ipswich 2017 | 88.6 | 23 | 10 | 87 | 116 | 143 |
| | | | 25 | 15 | 20 | 24 |
| | | | 50 | 5 | 6 | 7 |
| Brackenhurst 2018 | 5.3 | 30 | 10 | 144 | 193 | 238 |
| | | | 25 | 24 | 32 | 39 |
| | | | 50 | 7 | 9 | 11 |
| Brighton 2018 | 13.9 | 31 | 10 | 152 | 202 | 250 |
| | | | 25 | 26 | 34 | 41 |
| | | | 50 | 8 | 10 | 12 |
| Brackenhurst 2017 | 3.9 | 38 | 10 | 234 | 312 | 386 |
| | | | 25 | 39 | 51 | 63 |
| | | | 50 | 11 | 14 | 17 |

### *3.3.2 Resource costs*

The REM had high start-up costs, principally due to the initial purchase of cameras (£6,400; Table 3.8). Higher start-up costs are also required in urban (£10,630) versus rural (£8,532) areas because of the differences in labour costs: human resources required to carry out urban surveys (468 hours) were, on average, 2.3 times higher than in rural sites (200 hours) due to the need to carry out community engagement and to process a higher number of videos. However, as camera traps are reusable, any subsequent site survey would only need to cover labour costs, decreasing expenditure per site to £3,664 and £1,566 in urban and rural areas, respectively. Survey length in urban sites (46 ± 1 days) was higher than in rural (23 ± 5 SE) sites due to the need to enlist the help of householders.

Table 3. 8. Resources required to estimate hedgehog densities in urban and rural landscapes using camera trapping and the Random Encounter Model. Hours of labour are average values obtained from rural (n=3) and urban (n=4) sites required to carry out community engagement, fieldwork and data analysis; associated costs are based on the national minimum UK wage (£7.83/hour).

| Category | Description | Urban | | Rural | |
|---|---|---|---|---|---|
| | | Units | Cost | Units | Cost |
| Equipment | Camera traps | 40 | 6400 | 40 | 6400 |
| | Memory cards/batteries | 40 | 354 | 40 | 354 |
| | Padlocks/chains | 40 | 212 | 40 | 212 |
| | Sub total | £6,966 | | £6,966 | |
| Labour (hours) | Community engagement | 150 | 1175 | - | - |
| | Field work | 268 | 2098 | 160 | 1253 |
| | Data analysis | 50 | 392 | 40 | 313 |
| | Sub total | £3,664 | | £1,566 | |
| TOTAL | | £10,630 | | £8,532 | |

## 3.4 Discussion

The three methods used in this study (nocturnal capture-recapture data analysed using SCR, camera trap data analysed using site-specific parameters within a random encounter model (ssREM), and camera trap data analysed using averaged REM parameters (aveREM)) generated similar estimates of hedgehog density, regardless of

whether they were employed in urban or rural landscapes. However, only the aveREM is potentially amenable for inclusion as part of any future citizen science-based national survey of hedgehogs in the UK, as nocturnal spotlight counts require surveyors to be out at night, raising health and safety concerns, and require animals to be caught, marked and re-caught, requiring extensive training and licensing. In addition, using citizens to collect site-specific data from video recordings is fraught with technical difficulties as measurements must be taken accurately to obtain robust estimates of hedgehog density. An averaged parameter approach, where citizen surveyors only need to record hedgehog sightings, would circumvent this issue, as well as significantly reducing the time required to analyse the resultant data. Furthermore, the aveREM methodology was associated with high statistical power, being capable of detecting population changes of 25% with a power of >0.90.

The aveREM method is, however, associated with significant start-up costs through the purchase of camera traps, memory cards, batteries and other ancillary equipment, and also community engagement costs. Yet, many of these are one-off costs. By 'recycling' cameras between successive survey locations, the survey cost per site is diminished. For example, hedgehogs can be surveyed from April-October inclusive (Williams et al., 2018a). Given that sites were surveyed, on average, for 25 nights (4 sets of 30 CTLs per site, with a mean of 6 nights per CTL), this would indicate that each set of cameras could be used to survey 7 sites a year, and can be used over multiple years.

Additional cost savings could be made by using volunteer surveyors to carry out all community engagement exercises. This would include contacting landowners/householders, deploying and re-deploying cameras, and downloading and reporting data (Appendix A). This would be a significant commitment on the part of any volunteer, although a recent national survey of hedgehogs in England and Wales demonstrated that the surveyors still obliged, despite the large commitment (Williams et al., 2018a). Furthermore, within urban areas, it might be possible to enlist the help of groups of volunteers within the vicinity of a single study site.

A single network of cameras may enable multiple species to be recorded simultaneously (Burton et al., 2015). Caravaggi et al. (2016) used the REM approach for quantifying, in the same study, densities of Irish hares (*Lepus timidus hibernicus*) and European hares

(*L. europaeus*). Consequently, the aveREM approach has potential for future monitoring, not only of hedgehog populations, but also a wide range of other species.

The hedgehog densities estimated in this study in both urban (13.9-25.9 $km^{-2}$; Ipswich 2017 excluded – see below) and rural landscapes (1.2-6.8 $km^{-2}$) compare favourably with those from other studies in the UK and Europe. For example, Dowding (2007) and Hubert et al. (2011) recorded densities of 17 $km^{-2}$ and 36.5 $km^{-2}$ in urban sites in England and France, respectively, whilst Parrott, Etherington and Dendy (2014), Hubert et al. (2011) and Young et al. (2006) recorded densities in rural locations of 4 $km^{-2}$, 4.4 $km^{-2}$ and 9 $km^{-2}$, respectively. In addition, Parrott, Etherington and Dendy (2014) reported a density of 47 $km^{-2}$ based on surveys of amenity fields (recreation grounds, sports grounds, village green) only, but how this relates to hedgehog density in wider areas of human habitation is not known. Whilst this concordance is potentially reassuring, one important caveat is that, because of the inherent difficulties associated with studying wild hedgehog populations, true population size in all studies, including ours, is not known. What these data do indicate clearly, however, is that densities are much higher in urban sites that have been surveyed, likely due to favourable environmental conditions such as higher food availability including supplementary feeding (Hubert et al., 2011; Pettett et al., 2018) and decreased risk of predation by badgers (Young et al., 2006; Trewby et al., 2014; Pettett et al., 2017b).

### *3.4.1 Limitations and recommendations*

Despite its apparent potential, the REM methodology may be associated with some constraints that need to be considered and addressed. First, based on the results of this study, the REM could not be implemented at one site (Sutton Bonington) as the population was very low (only two animals were captured during nocturnal spotlight surveys), and only one camera recorded hedgehogs. However, this could be resolved by deploying cameras for longer, expanding the area of survey sites and/or increasing camera density to achieve Rowcliffe et al.'s (2008) recommendation of a minimum of 10 independent captures. The first two options would potentially impact the assumption that populations are closed as hedgehogs may breed throughout much of the year, with males making exploratory movements in search of females, and juvenile animals being recruited (Morris, 2006). However, if densities change during the survey, the REM will estimate densities averaged across the trend (Rowcliffe et al., 2008), so these

approaches are likely to be viable. The SCR methodology is also quite robust for violations of the closure assumption (Dupont et al., 2019), so estimates here are expected to be reliable.

Second, our findings suggest that behaviour of hedgehogs in urban areas are likely influenced by differences in buildings density, as shown in urban red foxes (Harris and Rayner, 1986). Such behaviour might have influenced the density estimates produced by the methodologies implemented here. For example, despite both the aveREM and SCR producing high densities with large confidence interval in Ipswich West, the aveREM produced densities two times greater than the corresponding SCR estimate. The difference between the aveREM and SCR estimates could be due to habitat structure and hedgehog behaviour as Ipswich West was a highly urbanised area, containing the greatest proportion of built-up land and the smallest proportion of gardens (Table 2.2), which were mainly back gardens. The preference of hedgehogs for back gardens in urban areas (Dowding et al., 2010) could have made the difference in the areas surveyed by both methods more prominent in highly urbanised areas: data analysed by SCR was mainly collected on roads and front gardens, while the REM data was mainly collected in back gardens. In our study design, cameras were mainly placed in back gardens to avoid theft and damage, and this has probably affected the random placement of cameras. This limitation is likely to be encountered in any camera trapping study in urban areas. The study design used here is robust and can work across a range of rural/urban landscapes, and with different housing densities in urban areas. However, understanding landscape structure and habitat preference will allow researchers to evaluate the impact of these features when estimating densities using the REM.

### 3.5 Conclusion

Remote sensing techniques are increasingly being used as part of citizen science projects to monitor wildlife on large spatial scales (e.g., Swanson et al., 2015; McShea et al., 2016). Involving the general public allows data to be collected from areas that would otherwise be difficult to access, and costly to survey (Parsons et al., 2018 ). This study is the first to test the Random Encounter Model (REM) to study small mammals across a range of landscapes, and our results indicate that an approach based upon averaged parameters is potentially a suitable method for estimating hedgehog density across both urban and rural habitats, and one that is capable of detecting a 25% change in

population size with high statistical power. It is also an approach where citizen scientists could be recruited to collect robust field data, thereby reducing costs and increasing sample sizes. The use of motion-activated cameras would also enable the monitoring of multiple species in both landscapes. However, further studies on a wider range of species are required across the broad range of urban and rural habitats/landscapes to derive suitable average parameters for inclusion in any national monitoring program.

# CHAPTER FOUR

# Space-use of hedgehogs in urban and rural landscapes

## 4.1 Introduction

Understanding the spatiotemporal distribution of animals is of key importance in population and behavioural ecology (Spencer, 2012). Knowing where and when animals are, allows research to be undertaken into why animals utilise various spaces, and to predict where else they could occur (Guisan and Zimmermann, 2000; Scott et al., 2002). This knowledge is needed to deliver effective population management and conservation of species (Aarts et al., 2008).

The spatiotemporal distribution patterns of animals are a result of individual movement processes (Van Moorter et al., 2016). These processes can play an essential role in the survival of individuals and evolution of species, affecting the dynamics of populations and communities and, ultimately, the function of ecosystems (LaPoint et al*.,* 2015). Most organisms restrict their movement to well-defined areas (Burt, 1943) which are often studied using the home range concept, where the home range is an area that an individual uses, but does not defend, over a given period of time (Burt, 1943; White and Garrott, 1990; Millspaugh and Marzluff, 2001). The home range is the most common space-use estimator in ecological research (Börger et al., 2006), as it can link animal movement to the distribution of resources for survival and reproduction (Börger, Dalziel and Fryxell, 2008), allowing a better understanding of the covariates governing animal space-use.

Movement behaviour of organisms is influenced by the internal state (i.e., motivation to move), motion (i.e., ability to move) and navigation capacities (i.e., ability to orientate and navigate the landscape) of individuals, alongside external environmental factors such as landscape, weather and the presence of other individuals (Nathan et al., 2008). When animals navigate in space and time, they have the ability to process and respond to information related to the structure and dynamics of the environment (Nathan et al., 2008). For example, the distribution of resources in the landscape is a well-known predictor of animal space use: when resources are unpredictable and widely distributed, organisms disperse over larger distances to meet their needs (Macdonald, 1983). Given

that resource distribution can be dynamic, animal movements can also change. Therefore, identifying how environmental factors define animal movement (Aarts et al., 2008) is vital to promote habitat connectivity, thus the movement of organisms. This is especially important in highly heterogeneous landscapes such as cities and towns (Faeth et al., 2005), as poor habitat connectivity can isolate individuals, leading to genetic drift and risking population persistence (Lefkovitch and Fahrig, 1985; Johnson and Munshi-South, 2017)

Understanding animal movement in human-dominated landscapes is of current interest to wildlife biologists to investigate how species can adapt to these rapidly-changing landscapes (Grinder and Krausman, 2001; LaPoint et al., 2015; Mäkeläinen et al., 2016; Zeller et al., 2019). Urbanisation increases habitat loss and fragmentation (McDonnell and Hahs, 2015) and, while the impact of habitat loss on wildlife is usually immediate, the effect of fragmentation is less direct and can take several generations to manifest (Parris, 2016). Habitat fragmentation changes not only the diversity and structure of the community, but also the movement of organisms and resources among natural patches (James, 2018). Physical barriers also have a high impact on terrestrial species, isolating populations in the remaining patches of suitable habitat and, therefore, affecting dispersal (Parris, 2016).

Urbanisation affects the movement and space-use of mammals. Smaller home ranges in urban areas have been reported worldwide among the most common urban mammals: red fox *Vulpes vulpes*, grey fox *Urocyon cinereoargenteus*, coyote *Canis latrans*, bobcat *Lynx rufus*, raccoon *Procyon lotor*, striped skunk *Mephitis mephitis*, Eurasian badger *Meles meles,* stone marten*, white-tailed deer Odocoileus virginianus,* and woodchuck *Marmota monax* (Gosselink et al., 2003; Atwood, Weeks and Gehring, 2004; Storm et al., 2007; Lehrer and Schooley, 2010; Šálek, Drahníková and Tkadlec, 2015; Ellington and Gehrt, 2019). The main factors responsible for reducing home range size in urban areas are (1) the degree of urbanisation, and consequent increase in fragmentation and traffic volume, which reduces movement and dispersal of individuals (Atwood, Weeks and Gehring, 2004; Rondinini and Doncaster, 2002; Ellington and Gehrt, 2019), and (2) resource availability (Atwood, Weeks and Gehring, 2004; Prange, Gehrt and Wiggers, 2004; Šálek, Drahníková and Tkadlec, 2015), where species benefit from high and predictable resources such as food waste and supplementary feeding and, therefore, do

not need to cover large areas to meet their daily requirements (Contesse et al., 2004; Prange, Gehrt and Wiggers, 2004; Davies et al., 2009; Davison et al., 2009). The resources available in urban landscapes not only influence the areas individuals need to range but, at a population level, affect the density of individuals that an area can sustain. Indeed, several studies have shown that some species have higher densities in urban areas (McKinney, 2006; This study - see Chapter 3). However, our understanding of urban populations remains limited as studies comparing urban and non-urban populations are difficult to undertake due to the challenges of surveying urban areas where most land is privately owned (Schaus et al., 2020).

The West European hedgehog occupies urban and rural habitats (Hof and Bright, 2016; Williams et al., 2018a; b), hence, it is a good model species to investigate the effect of urbanisation on space-use behaviour. Recent studies have suggested that density (Schaus et al., 2020) and occupancy (Williams et al., 2018b) of hedgehogs is positively related to urban areas, which is likely due to abundant human-related food resources (Hubert et al., 2011; Pettett et al., 2018), decreased risk of predation by badgers (Young et al., 2006; Trewby et al., 2014; Yarnell et al., 2014; Pettett et al., 2017b), and favourable climatic conditions (Hubert et al., 2011). However, despite the apparent beneficial effect of urbanisation on hedgehog populations, few studies have investigated the space-use behaviour of hedgehogs in urban landscapes. This may provide key information about the population persistence, especially as dispersal and long-distance movement are an essential part of the species' ecology (Morris, 2018).

Previous studies have identified a difference in the space-use and movement behaviour of hedgehogs in relation to sex, where males have larger home ranges and travel further distances per night than females (Reeve, 1982; Riber, 2006; Dowding et al., 2010; Haigh, O'Riordan and Butler, 2013; Rautio, Valtonen and Kunnasranta, 2013; Rodriguez Recio et al., 2013). The difference in home range size between males and females is also influenced by time of year (Reeve, 1982; Riber, 2006; Dowding et al., 2010; Haigh, O'Riordan and Butler, 2013; Rautio, Valtonen and Kunnasranta, 2013; Rodriguez Recio et al., 2013): males can have home ranges up to four times larger during the peak breeding activity (Rodriguez Recio et al., 2013), to cover the range of as many females as possible. This sex-related movement behaviour has also been reported in juvenile individuals (Rasmussen et al., 2019).

External factors, such as weather condition, also impact animal movement (Price-Rees et al., 2014; Sadoti et al., 2017; McLester et al., 2019). For example, temperature and rainfall can impact prey availability (Crawford-sidebotham, 1972; Edwards and Lofty, 1977; Honěk, 1997; Whalen, Parmelee and Edwards, 1998), and Dowding (2007) found that nightly activity, speed and range of hedgehogs, showed a positive association with temperature due to the increased activity of invertebrate prey at warmer temperatures. Predation risks also play a crucial role in shaping the movement of hedgehogs, as seen by the spatial avoidance of the European badger setts (Ward, MacDonald and Doncaster, 1997; Pettett et al., 2017a; b). The urban infrastructure may also restrict movement with the potential of roads to act as barriers to hedgehogs (Doncaster, Rondinini and Johnson, 2001; Rondinini and Doncaster, 2002; Dowding et al., 2010).

Although urban areas are generally associated with higher densities of hedgehogs, there is growing concern that hedgehog populations may be declining in both urban and rural environments due to habitat fragmentation and poor habitat connectivity at varying spatial scales. A recent study by Williams et al. (2018a) showed that hedgehogs only occupied 22% of 1km squares in rural England and Wales, suggesting that much of the wider countryside is potentially unsuitable for hedgehogs, disrupting connectivity and persistence between neighbouring populations. In urban habitats, occupancy is also low; only 37% of gardens in Reading were visited by hedgehogs over 5 days (Williams et al., 2018b), suggesting that not all gardens in residential areas are accessible to, or used by, hedgehogs, potentially reducing carrying capacity and further risks to the persistence of smaller populations. Such assumptions are supported by genetic studies of rural populations (Becher and Griffiths, 1998) and more recent studies on genetic divergence due to roads and river barriers in Zurich (Braaker et al., 2017). By contrast, a lack of genetic divergence in Berlin has been attributed, in part, to high levels of connectivity facilitated by many green spaces across the city (Barthel, 2019). As such, urban green areas, such as gardens and parks, can facilitate animal movement in fragmented landscapes (Angold et al., 2006; LaPoint et al., 2013; Hämäläinen, Fey and Selonen, 2018), acting as stepping stones connecting habitat patches and resources (Spellerberg and Gaywood, 1993; Bennett, 2003), facilitating gene flow and genetic connectivity.

To date, the majority of hedgehog movement studies have focused on either urban or rural landscapes (e.g., Rodriguez Recio et al., 2013; Braaker et al., 2014; Rast, Barthel

and Berger, 2019). Consequently, the insights gained from single-landscape studies may lead to poor inference about movement patterns across the wider distribution. Therefore, comparative studies across urban-rural gradients are needed to provide a better understanding of hedgehog space-use behaviour, the area requirements for individuals and populations, and how these vary spatially and temporally.

This study aims to identify factors that affect nightly short term space-use behaviour of hedgehogs in urban and rural landscapes, across England. Specifically, the role of sex, weather condition and habitat features, in determining hedgehog space-use behaviour. An information theory approach (Burnham and Anderson, 2002) is used to compare a series of *a priori* alternative models of nightly home range size, including variables where previous research indicated an influence on movement and space-use behaviour of hedgehogs and other urban species. The outcomes of this study will improve our understanding of the key elements influencing the space-use behaviour of ground-dwelling mammals across a range of landscapes, allowing conservation actions to be implemented across a gradient of human-modified landscapes.

## 4.2 Methods

### *4.2.1 Animal telemetry*

Spotlight surveys were carried out at five rural and four urban sites across England between 2016 and 2019 (Figure 2.1; Table 2.1) to find and capture adult hedgehogs. A Global Positioning System with Very High Frequency (GPS/VHF) tag (hereafter termed 'tag') (model: Biotrack PinPoint 240; Biotrack Ltd, Dorset, UK) was attached to each hedgehog to monitor space-use and movement. Spotlight surveys to find and tag hedgehogs took place at night along pre-defined transects, across publicly accessible land (i.e., main and secondary roads, footpaths, and around field margins). Hedgehogs were captured by hand, weighed (g) using an electronic balance (Salter 1035 platform scale) and sexed according to Morris (2006). Animals were classified as adults if they weighed >600g (Young et al., 2006; Haigh 2011; Hubert et al., 2011). Tags were glued directly to a dorsal midline patch of clipped spines on the hedgehog (Glasby and Yarnell, 2013). Tags weighed 10g, <5% of the hedgehog's body mass, following the guidelines of the American Society of Mammalogists (Sikes and Gannon, 2011). Each tagged hedgehog's weight, health and tag attachment was checked after 24 hours, then every 4 days, to ensure that the tag was not compromising the individual's welfare.

### *4.2.2 GPS data processing*

To obtain fine-scale spatiotemporal data, tags were programmed to record location fixes every five minutes during the night. Data collection started one hour after sunset and one hour before sunrise, as this was regarded as the time when hedgehogs are most active, and tags remained on the hedgehogs for at least five nights. Data collected by the tags included the date, time, geographic coordinates, Horizontal Dilution of Position (HDOP), location error (eRes) and the number of satellites used to obtain a fix. Prior to home range analysis, location data (GPS fixes) were screened for inaccuracies following the manufacturer's recommendations: GPS fixes with HDOP >5, eRes >10 and satellites ≤ 4 were removed. Distance travelled was calculated using the Euclidian (i.e., straight line) distance between two consecutive locations, and implausible locations and hedgehog speeds (i.e. over 1 m/s) were also removed (Braaker et al., 2014).

### *4.2.3 Garden use*

Gardens are important habitats for hedgehogs, as these provide shelter, nest sites and other vital resources for survival (Ryall and Hatherell, 2003; Hubert et al., 2011; Yarnell et al., 2014; Williams, Stafford and Goodenough, 2015). Therefore, garden use was investigated on three temporal scales: (a) per night, (b) during the whole tracking period of each individual and (c) during the whole tracking period of all individuals at each study site. The proportion of gardens used was assessed by dividing the number of gardens that were visited (i.e., where GPS fixes were recorded) by the total number of gardens found in the habitat available. Habitat available was calculated by creating a 100% minimum convex polygon (MCP) around the GPS fixes recorded on the three different temporal scales: (a) the proportion of gardens used per night, per individual (nightly level); (b) all GPS fixes generated by each individual (individual level), and (c) all GPS fixes generated at each survey site by all individuals (site level). The difference in garden use was compared between males and females, urban and rural landscapes, and between the different sites.

### *4.2.4 Home range methodology*

Recent advances in telemetry technology now allow researchers to monitor animal movement continuously, producing high volume, accurate and precise, location data (Cagnacci et al., 2010; Hebblewhite and Haydon, 2010; Tomkiewicz et al., 2010). However, these advantages challenge the validity of well-established data analysis

methods (Gaillard et al., 2010; Kie et al., 2010; Thurfjell, Ciuti and Boyce, 2014). For example, Minimum Convex Polygons (MCP) and Kernel Density Estimators (KDE), the most common methods to study home range, generally treat locations as independent events, an assumption that is violated with high frequency sampled movement data (Lyons, Turner and Getz, 2013). While some techniques have been developed to consider such autocorrelated data (Harris et al., 1990; Rooney, Wolfe and Hayden, 1998), others have been developed to take advantage of this information by modelling the movement between locations (Horne et al., 2007; Benhamou and Cornélis, 2010). Despite these movement-based home range methods incorporating information containing temporal autocorrelation, they only model space use. Consequently, Lyons, Turner and Getz (2013) proposed the Time Local Convex Hull (T-LoCoH) method, which builds upon the Local Convex Hull method (LoCoH; Getz and Wilmers, 2004) by integrating time with space in the calculation of home range and utilisation distribution (UD).

The LoCoH method adopts concepts of the minimum convex polygon (MCP) and non-parametric kernel density estimation (KDE) methods (Getz et al., 2007). LoCoH finds the nearest neighbours of each data point and, using the MCP method, constructs local convex polygons (i.e., hulls). To obtain a UD, hulls are arranged and merged from smallest to largest, producing a series of nested polygons that reflect the relative density of locations. Therefore, LoCoH estimates UD arising directly out of the data, unlike parametric kernels that have a form dependent upon the shape of the kernel function and the chosen bandwidth (Lyons, Turner and Getz, 2013). By estimating UD directly from the data, the LoCoH method produce UDs that capture physical edges in the landscape (e.g., lakes, fence lines) and temporal boundaries in space use (Lyons, Turner and Getz, 2013).

The LoCoH algorithm starts by identifying a set of nearest neighbours for each point using three possible methods (Getz et al., 2007): the *k*-method finds the $k^{th}$ nearest neighbours around each point; the *r*-method takes all points within a fixed radius r; the adaptive *a*-method selects all points whose cumulative distance to the parent point, ordered smallest to largest, is less than or equal to *a*. The values of *k*, *r* and *a* need to be specified by the user. Once the nearest neighbour has been identified, local convex hulls are constructed around each point, and its nearest neighbours, and hulls are merged.

The union hulls, covering x% of points, provide the construction of the x% isopleth. Home ranges are usually quantified as the 95% isopleth of the estimated UD ($UD_{95}$), and areas that are intensively used by an individual to meet its requirement are often referred as 'core areas' and are defined as the region contained within the 50% isopleth of the UD ($UD_{50}$).

T-LoCoH (Lyons, Turner and Getz, 2013) is an extension of the LoCoH algorithm that incorporates the time stamp of each point and uses a time-scaled distance factor (*s*) in the selection of the nearest neighbour and merging the hulls. In the identification of the nearest neighbours, *s* plays a role in differentiating points that are far away in time, even though they might be close in space: when *s*=0, time is not considered. As *s* increases, time plays an increasingly important role, eventually restricting neighbour selections purely on time. Lyons, Turner and Getz (2013) recommend that the value of *s* should ensure that 40-60% of hulls are constructed using temporally correlated GPS fixes so that both the spatial and temporal data are considered relatively equal in the analysis.

### *4.2.5 Home range estimation*

Individuals were tracked over a short period due to the limited battery life of the GPS tags. The total number of nights the tags were attached to individuals varied between 5 and 15. Data exploration showed that the 100% MCP home-range area curve asymptote was only reached for 4 individuals (3 rural, 1 urban) out of 52. Therefore, to allow a fair comparison of space-use between landscapes, nightly home ranges were calculated. The T-LoCoH method (Lyons, Turner and Getz, 2013) was used to calculate 95% isopleths to identify nightly home ranges and 50% isopleths to identify core areas while active. For consistency, the value of *s* was set to ensure that 50% of the hulls were constructed from time-sequential locations (Stark et al., 2017). The *a*-method was used to choose the nearest neighbours; the value of *a* was set as the maximum displacement between two points in the movement data set (Getz et al., 2007). Analyses were performed using the R package *tlocoh* (Lyons, Turner and Getz, 2013). The 100% MCP was also calculated to allow comparison with other studies that have calculated total 100% MCP home range size.

### *4.2.6 Home range predictors*

An information theory approach was used to formulate 13 biologically-plausible models comprising 8 explanatory variables related to sex, landscape, weather, and habitat

characteristics (Table 4.1). Weather data, i.e., daily precipitation and minimum temperature, were obtained from the closest weather station to each study site (UK Meteorological Office: www.metoffice.gov.uk).

Using OS Mastermap Topography Layers and high resolution (25 cm) Vertical Aerial Imagery (EDINA Digimap Ordnance Survey Service, 2017), four characteristics of the habitat available (nightly level) were extracted for each nightly home range: (a) density of buildings per hectare, as a proxy for the degree of urbanisation and habitat complexity (Theobald, 2005, 2010; Robins et al., 2019); (b) total number of gardens used; (c) average size of those gardens (ha) and (d) the proportion of gardens used [values range from 0, none, to 1, all]. The proportion of gardens used was included to evaluate the cost associated with accessing resources (i.e., the trade-off between accessing gardens and the cost associated with travelling to access these resources). It is predicted that in areas with a high proportion of gardens used, hedgehogs will have smaller home ranges than areas with a low proportion. The variables related to building density and number and size of gardens accessed were positively skewed, therefore, standardised using z-scores prior to analysis (Norman and Streiner, 2014).

Following Zuur, Leno and Elphick (2010), data were examined for outliers in the response and explanatory variables, homogeneity and zero inflation in the response variables, collinearity between explanatory variables, and the nature of relationships between the response and explanatory variables. Outliers in the response variable (nightly home range) were detected that exceeded three standard deviations of the mean (Jones, 2019): these were assumed to be exploratory or dispersal events (Burt, 1943), so were removed from analyses.

A random intercept for individual hedgehogs was included in all models to introduce a correlation structure between observations for the same individuals (Bolker et al., 2009). To model 95% home range size, a gamma Generalised Linear Mixed Model (GLMM) was fitted, as home range size data were continuous, strictly positive and positively skewed (Zuur et al., 2009). Models were fitted using the package lme4 (version 1.1-21; Bates et al., 2015) in R (version 3.6.1; R Development Core Team, 2019). The best-fitting model was identified using Akaike's Information Criterion (AIC; Burnham and Anderson, 2004).

### *4.2.7 Home range overlap*

To illustrate how hedgehogs move through their home range, and evaluate how intensive their home range is used, the percentage of the nightly home range ($UD_{95}$) overlap was calculated on subsequent nights for each individual. Although limited by the small number of days that data is derived, nightly overlaps are useful for understanding how hedgehogs move on consecutive days through habitats and to illustrate any barriers to movement or unused areas in the immediate landscape. Although some degree of overlap is expected, i.e., hedgehogs are known to re-use the same nests on consecutive nights (Rast, Barthel and Berger, 2019), a high percentage of home range overlap will indicate that the individuals are constantly reusing the same areas, which could be due to the resource availability or movement restrictions.

All spatial queries were performed in ArcGIS 10.3.1 (ESRI, 2015). All results are given as mean ± SD unless stated otherwise.

Table 4. 1. *A priori* models for the home range sizes of West European hedgehogs (*Erinaceus europaeus*). '+' represents the additive effect of covariates on home range sizes.

| Model | Model formulation | Model interpretation | Explanatory covariate source |
|---|---|---|---|
| M00 | Null | No variables | |
| M01 | Sex (female, male) | Area ranged will vary between males and females | Riber, 2006; Haigh, O'Riordan and Butler, 2013 |
| M02 | Landscape (urban, rural) | Area ranged will vary between urban and rural landscapes | Riber, 2006; Haigh, O'Riordan and Butler, 2013; Rautio, Valtonen and Kunnasranta, 2013; Rasmussen et al., 2019 |
| M03 | Buildings density | Area ranged will be affected by habitat complexity | Storm et al., 2007; Lehrer and Schooley, 2010; Šálek, Drahníková and Tkadlec, 2015 |
| M04 | Daily precipitation (mm) + Minimum temperature | Area ranged will be influenced by prey availability, which is affected by climatic conditions | Dowding et al., 2010 |
| M05 | Number of gardens used | The presence of gardens will affect the total area ranged, as hedgehogs strongly select these habitats | Dowding et al., 2010; Haigh, O'Riordan and Butler, 2013; Pettett et al., 2017a |
| M06 | Average garden size used | The size of the gardens accessed will influence the area needed to range per night as this habitat provides food sources. | Baker and Harris, 2007 |
| M07 | Proportion of gardens used | The trade-off between accessing resources and travel costs will affect area ranged | This study |
| M08 | Sex + Landscape | Area ranged will be influenced by sex and landscape | |
| M09 | Sex + Landscape + Daily precipitation (mm) + Minimum temperature | Area ranged will be influenced by sex, landscape and climatic conditions | |
| M10 | Sex + Landscape + Number of gardens accessed | Area ranged will be influenced by sex, landscape and number of gardens accessed | |
| M11 | Sex + Landscape + Buildings density | Area ranged will be influenced by sex, landscape, and complexity of habitat | |
| M12 | Sex + Landscape + Proportion of gardens used | Area ranged will be influenced by sex, landscape, and the trade-off between accessing resources and travel cost | |
| M13 | Sex + Landscape + Average garden size accessed | Area ranged will be influenced by sex, landscape and size of gardens visited | |

## 4.3 Results

Fifty-two individual hedgehogs were tagged across 11 sites, comprising 29 (13 males and 16 females) in urban and 23 (9 males and 14 females) in rural areas (Table 4.2). The distribution of the GPS fixes collected across each study site (n=11) are provided in maps in Appendix B. Maps with the GPS fixes recorded at each site and the movement paths followed by each individual (n=52) on each night, are provided in Appendix C and D, respectively. On average, tags remained on individuals for 9.8 ± 2.3 days (range: 5-15; Table 4.2). A total of 37 699 locations (GPS fixes) were recorded, of which 9 563 were removed due to low confidence in fix accuracy, leaving 28 136 GPS fixes. However, if an animal was captured in the middle of the night, GPS fixes of that night were removed to account for complete nights that individuals were active. Therefore, the number of GPS fixes available from which to conduct analyses was 24941.

Table 4. 2. Number of GPS tags deployed on West European hedgehogs (*Erinaceus europaeus*) and the average tracking period (i.e., number of days the tags remained on the individuals) across urban (n=5) and rural (n=6) habitats between 2016 and 2019, in England. . SD= Standard Deviation

| Landscape | Site | GPS tags deployed | | | | No. of tracking days | |
|---|---|---|---|---|---|---|---|
| | | Males | Females | Sub-total | Total | Average ± SD | Total |
| Rural | Hartpury 2017 | 2 | 2 | 4 | 23 | 8.5 ± 2.4 | 9.4 ± 1.2 |
| | Brackenhurst 2017 | 1 | 3 | 4 | | 9.3 ± 1.3 | |
| | Brackenhurst 2018 | 2 | 3 | 5 | | 10.8 ± 2.5 | |
| | Sutton Bonnington 2018 | 0 | 1 | 1 | | 10 ± 0 | |
| | Bishop Burton 2019 | 3 | 3 | 6 | | 10 ± 0 | |
| | Riseholme 2019 | 1 | 2 | 3 | | 10 ± 0 | |
| Urban | Southwell 2016 | 3 | 3 | 6 | 29 | 12.3 ± 1.5 | 9.6 ± 2.6 |
| | Ipswich 2017 | 1 | 3 | 4 | | 7.3 ± 1.3 | |
| | Ipswich 2018 | 5 | 1 | 6 | | 6.7 ± 1.8 | |
| | Brighton 2018 | 4 | 3 | 7 | | 10 ± 2.1 | |
| | Brighton 2019 | 3 | 3 | 6 | | 11.7 ± 2 | |
| Total | | 25 | 27 | 52 | | 9.8 ± 2.3 | |

Initial capture weight of urban hedgehogs (841 ± 145g) was not significantly different to rural hedgehogs ( 897 ± 122g) (t = 1.51, df = 49.77, p = 0.14), neither was the weight of males (886 ± 148g) significantly different to that of females (846 ± 126g) (t = -1.06, df = 47.32, p = 0.30; Table 4.3). A significant but weak positive correlation was found between the initial capture weight of individuals and the mean nightly area ranged during its tracking period ($r_{s\ (50)}$ =0.35, p <0.05; Figure 4.1).

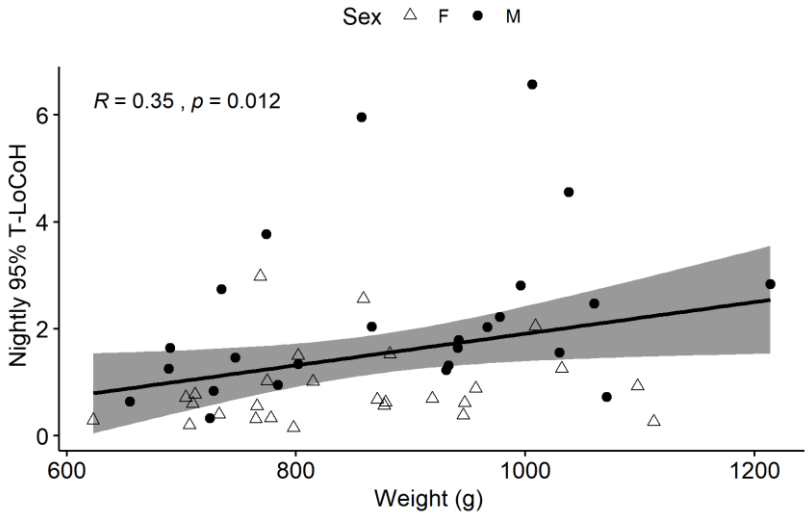



Figure 4. 1. Correlation analysis showed that the weight of hedgehogs was positively correlated with Nightly 95% T-LoCoH nightly (R=0.35, p=0.012). Spearman's correlation test was used (p<0.05 significance; R=correlation coefficient).

Weight (g) change over the tracking period varied, with 28 individuals increasing and 19 decreasing in weight (Appendix E). Mean percentage weight change during the tracking period was + 2.9 ± 9.5 %, with males increasing on average 3.6 ± 10.4 %, but not significantly different to females (+ 2.3 ± 8.8 %) (t = -0.44, df = 39, p = 0.66). Rural (1.7 ± 8.3 %) and urban (3.9 ± 10.5 %) hedgehogs did not show a significant difference in the proportion of weight change during the tracking period (t = -0.83, df = 45, p = 0.41). Finally, the mean weight of the individuals before and after the tag attachment was not significantly different (Paired t = -1.74, df = 46, p-value = 0.09), suggesting no negative impact of tag attachment on the individuals.

A significant difference between the total straight line distance between GPS fixes (m) travelled per night was found between males (1362 ± 662 m) and females (994 ± 419 m) (Mann-Whitney U test: U ($N_{males}$=224, $N_{females}$=224) = 16375; $p<0.05$); and between urban (970 ± 501 m) and rural hedgehogs (1397 ± 585 m) (U ($N_{urban}$=230, $N_{rural}$=218) = 37389; $p<0.05$), with males on average travelling further than females, and individuals in rural areas travelling further than those in urban areas. The recorded movement speeds (m/s) were also significantly higher in males (0.065 ± 0.025 m/s) than females (0.046 ± 0.015 m/s) (U ($N_{males}$=224, $N_{females}$=224) = 11279; $p<0.05$), and significantly higher in rural (0.0577 ± 0.0218 m/s) compared to urban (0.0531 ± 0.0239 m/s) (U ($N_{urban}$=230, $N_{rural}$=218) = 29662; $p<0.05$) landscapes.

Four male individuals (2 rural and 2 urban) appeared to make exploratory or potential dispersal movements exceeding ranges of 9 ha per night, over a total of 11 nights. The areas covered on these trips ranged from 10 to 19 ha per night and occurred between April and July. The average distance travelled on these exploratory trips was 3087 ± 632 m (range: 2116-4467); where larger distances were recorded by rural individuals (n=6; 3168 ± 688 m; range: 4468-2534) compared to urban individuals (n=5; 2989 ± 621m; range: 3736-2115). The weight of the urban individuals that carried out these exploratory trips was 1006 and 1214 g, above the average weight of urban males (856 ± 157g). The rural individuals that carried out these exploratory trips weighed 774 and 857 g, slightly below the average weight of rural males ( 925 ± 127g).

Table 4. 3. Summary of the weight of hedgehogs (*Erinaceus europaeus*) during the tracking period in urban and rural landscapes. Initial weight refers to the weight of capture and final weight when the GPS tag was removed. Weight variation was calculated by subtracting the initial from the final weight; positive values indicate an increase in weight. Values indicate the mean ± standard deviation and (in parenthesis) the number of observations. Weights are given in grams (g).

| Landscape | Initial weight (g) | | | Final weight (g) | | | Weight variation (g) | | |
|---|---|---|---|---|---|---|---|---|---|
| | Male | Female | Total | Male | Female | Total | Male | Female | Total |
| Rural | 925 ± 127 (9) | 878 ± 120 (14) | 897 ± 122 (23) | 926 ± 155 (8) | 892 ± 92 (14) | 904 ± 116 (22) | 7 ± 58 (8) | 13 ± 88 (14) | 11 ± 78 (22) |
| Urban | 856 ± 157 (16) | 811 ± 127 (13) | 841 ± 145 (29) | 908 ± 146 (13) | 824 ± 152 (12) | 868 ± 152 (25) | 39 ± 95 (13) | 18 ± 72 (12) | 29 ± 84 (25) |
| Total | 886 ± 148 (25) | 846 ± 126 (27) | 865 ± 137 (52) | 915 ± 146 (21) | 861 ± 125 (26) | 885 ± 136 (47) | 27 ± 83 (21) | 16 ± 80 (26) | 21 ± 81 (47) |

### *4.3.1 T-LoCoH home range*

For the 95% and 50% T-LoCoH calculations, all exploratory trips were removed, leaving 437 nightly home ranges. Mean nightly 95% home range was 1.43 ± 1.40 ha, ranging from 0.03 to 8 ha., and 50% core area was 0.51 ± 0.57 ha., with a range of 0.01 to 4.64 ha. (Table 4.5). Male nightly home range, $UD_{95}$ (1.95 ± 1.62 ha.) was significantly larger than females (0.93 ± 0.89 ha.; Mann-Whitney U test: U ($N_{males}$=213, $N_{females}$=224) = 13058; p<0.05). Rural hedgehogs (1.70 ± 1.55 ha.) had significantly larger home ranges than urban hedgehogs (1.17 ± 1.17 ha.) (U ($N_{urban}$=225, $N_{rural}$=212) = 30562; p<0.05; Table 4.6). Across all study sites, mean home ranges ($UD_{95}$) were significantly different across sites (Kruskal-Wallis rank-sum test: H(10) = 63.72, p<0.05), being largest in Riseholme (rural, 2.88 ± 1.84 ha.) and smallest in Ipswich 2017 (urban, 0.72 ± 0.88 ha.; Figure 4.2; Table 4.7). Figure 4.2 suggests that the difference in home range size between urban and rural landscapes could be influenced by the large home ranges reported at Riseholme. However, if removing Riseholme 2019 (n=33) from the comparison between urban and rural areas, there is still a significant difference between both landscapes (U ($N_{urban}$=225, $N_{rural}$=179) = 24459; p<0.05).

The core range ($UD_{50}$) showed similar patterns to the home range ($UD_{95}$) of those observed between males and females, between both landscapes and across the study sites. The number of GPS fixes used for the estimation of home and core ranges was similar across sex and habitat (Table 4.8), indicating that differences in the estimates of the home range were not due to an unbalanced sampling effort.

Considering the whole tracking period of each individual, the mean 100% MCP was not significantly larger in rural (17.4 ± 22.9 ha) compared to urban areas (13.9 ± 22.3) (Mann-Whitney U test: U ($N_{urban}$=29, $N_{rural}$=23) = 417; p=0.127). However, it was significantly larger for males (25.3 ± 28.9 ha) compared to females (6.37 ± 5.67 ha) (U ($N_{males}$=25, $N_{females}$=27) = 417; p<0.05). Nightly 100% MCP was significantly higher in rural (3.25 ± 3.27 ha) than in urban landscapes (2.38± 3.11 ha) (U ($N_{urban}$=225, $N_{rural}$=212) = 30275; p<0.05). Also, higher nightly 100% MCP was found in males (4.04 ± 4 ha) compared to females (1.63 ± 1.47 ha) (U ($N_{males}$=213, $N_{females}$=224) = 417; p<0.05; Table 4.7). The MCP method produced bigger areas than the T-LoCoH method, as the latter is able to detect and remove areas that are not used by individuals (Figure 4.3).

Table 4. 4. Nightly and total area ranges (ha) calculated for each individual (n=52) using the Minimum Convex Polygon (MCP) and Time Local Convex Hull (T-LoCoH) methods. For the MCP, 100% of the GPS fixes were used to calculate the area ranged on each night (nightly level) and during the whole tracking period of each individual (individual level). Individual level 100% MCP was used to investigate whether enough GPS fixes were collected to reach an asymptote. 50% and 95% of GPS fixes were used to calculate home range using the T-LoCoH method. For the 95% T-LoCoH, the percentage overlap between consecutive nights was also calculated. SD= Standard Deviation.

| Landscape | Site | Hedgehog ID | Sex | 100% MCP (ha) | | | | Nightly 50% t-LoCoH (ha) | | Nightly 95% t-LoCoH (ha) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Nightly | | Total | Asymptote reached | Mean | SD | Mean | SD | Nightly overlap | |
| | | | | Mean | SD | | | | | | | Mean | SD |
| Rural | Bishop Burton 2019 | BlueA_M | M | 4.26 | 5.72 | 22.64 | No | 0.87 | 1.11 | 2.22 | 2.85 | 36.87 | 24.09 |
| | | BlueB_F | F | 2.07 | 0.80 | 6.33 | No | 0.41 | 0.10 | 1.25 | 0.53 | 53.14 | 18.71 |
| | | BlueC_M | M | 2.00 | 1.26 | 6.77 | No | 0.42 | 0.23 | 1.32 | 0.72 | 59.91 | 24.86 |
| | | BlueD_F | F | 1.52 | 0.54 | 4.61 | No | 0.40 | 0.13 | 0.88 | 0.32 | 38.25 | 15.81 |
| | | BlueE_F | F | 2.16 | 1.02 | 8.23 | No | 0.39 | 0.22 | 1.01 | 0.50 | 34.38 | 20.32 |
| | | BlueG_M | M | 3.77 | 1.68 | 12.11 | No | 0.60 | 0.27 | 2.04 | 1.40 | 15.06 | 18.03 |
| | Brackenhurst 2017 | BlackDD_F | F | 1.06 | 0.59 | 3.75 | No | 0.26 | 0.18 | 0.56 | 0.28 | 47.54 | 17.96 |
| | | BlackEE_F | F | 3.51 | 1.06 | 7.61 | No | 0.84 | 0.41 | 2.05 | 0.82 | 47.81 | 30.04 |
| | | BlackHH_F | F | 2.11 | 0.43 | 3.74 | No | 0.59 | 0.15 | 1.50 | 0.44 | 62.70 | 16.48 |
| | | BlueCC_M | M | 2.28 | 0.80 | 6.82 | No | 0.44 | 0.20 | 1.56 | 0.74 | 37.58 | 26.88 |
| | Brackenhurst 2018 | BlackDD_F | F | 1.24 | 0.67 | 5.58 | No | 0.29 | 0.14 | 0.72 | 0.27 | 40.94 | 25.90 |
| | | BlackEE_F | F | 1.22 | 0.73 | 7.96 | No | 0.24 | 0.18 | 0.62 | 0.32 | 25.85 | 18.01 |
| | | BlueAA_F | F | 0.60 | 0.21 | 2.11 | No | 0.20 | 0.16 | 0.40 | 0.15 | 40.09 | 34.38 |
| | | BlueCC_M | M | 7.07 | 4.06 | 33.50 | No | 0.74 | 0.43 | 2.48 | 1.07 | 26.90 | 21.27 |
| | | YellowAA_M | M | 6.55 | 3.02 | 72.45 | No | 1.33 | 0.74 | 3.77 | 1.65 | 48.82 | 31.33 |
| | Hartpury 2017 | BH_M | M | 13.10 | 5.63 | 96.53 | No | 1.80 | 0.86 | 5.95 | 1.44 | 8.08 | 10.52 |
| | | RA_M | M | 5.17 | 5.78 | 29.36 | Yes | 0.37 | 0.38 | 1.26 | 0.69 | 19.91 | 20.88 |
| | | RB_F | F | 2.32 | 1.81 | 13.91 | Yes | 0.27 | 0.26 | 1.02 | 0.58 | 11.12 | 12.82 |
| | | RH_F | F | 1.21 | 0.22 | 4.08 | No | 0.23 | 0.02 | 0.70 | 0.22 | 28.30 | 24.96 |
| | Riseholme 2019 | BlueA_M | M | 6.27 | 1.30 | 14.99 | No | 2.11 | 1.01 | 4.56 | 1.53 | 53.04 | 24.27 |
| | | BlueB_F | F | 4.51 | 1.78 | 15.04 | No | 0.82 | 0.96 | 2.56 | 1.76 | 49.88 | 27.89 |
| | | BlueC_F | F | 2.77 | 1.03 | 9.05 | No | 0.68 | 0.36 | 1.53 | 0.34 | 33.56 | 20.95 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Sutton Bonington 2018 | YellowA_F | F | 1.37 | 1.02 | 13.63 | No | 0.33 | 0.25 | 0.93 | 0.63 | 47.51 | 29.59 |
| Urban | Brighton 2018 | Blue_E_F | F | 0.59 | 0.32 | 2.70 | No | 0.13 | 0.09 | 0.33 | 0.14 | 14.44 | 14.00 |
| | | BlueA_M | M | 8.79 | 6.07 | 39.50 | Yes | 0.81 | 0.45 | 2.82 | 1.14 | 27.80 | 23.63 |
| | | BlueC_M | M | 2.68 | 1.68 | 23.01 | No | 0.46 | 0.44 | 1.35 | 0.86 | 19.65 | 17.86 |
| | | RedC_F | F | 0.20 | 0.08 | 0.57 | No | 0.07 | 0.03 | 0.15 | 0.06 | 61.51 | 16.88 |
| | | RedD_F | F | 0.35 | 0.11 | 0.89 | No | 0.09 | 0.06 | 0.26 | 0.09 | 56.70 | 27.84 |
| | | YellowA_M | M | 3.32 | 2.28 | 17.14 | No | 0.64 | 0.45 | 1.65 | 1.07 | 21.09 | 21.35 |
| | | YellowC_M | M | 2.50 | 0.88 | 5.34 | No | 0.52 | 0.27 | 1.46 | 0.52 | 41.12 | 18.82 |
| | Brighton 2019 | BlackA_M | M | 1.50 | 0.67 | 7.81 | No | 0.26 | 0.16 | 0.73 | 0.42 | 3.61 | 2.95 |
| | | BlackC_F | F | 1.65 | 0.64 | 13.75 | No | 0.20 | 0.10 | 0.77 | 0.39 | 7.99 | 12.62 |
| | | BlackD_M | M | 2.09 | 1.21 | 15.89 | No | 0.40 | 0.28 | 1.23 | 0.69 | 23.54 | 23.11 |
| | | BlueA_F | F | 1.28 | 0.31 | 4.00 | No | 0.24 | 0.12 | 0.63 | 0.32 | 23.63 | 16.28 |
| | | RedA_M | M | 8.29 | 5.79 | 50.55 | No | 0.98 | 0.49 | 2.84 | 1.42 | 24.92 | 30.99 |
| | | RedC_F | F | 4.83 | 1.96 | 25.19 | No | 0.99 | 0.86 | 2.98 | 1.05 | 18.68 | 21.65 |
| | Ipswich 2017 | BlueF_F | F | 1.01 | 0.46 | 3.78 | No | 0.17 | 0.08 | 0.56 | 0.21 | 12.41 | 13.53 |
| | | RedC_M | M | 2.90 | 2.35 | 13.75 | No | 0.73 | 0.82 | 1.79 | 1.51 | 29.11 | 14.67 |
| | | RedH_F | F | 0.88 | 0.37 | 3.45 | No | 0.27 | 0.12 | 0.60 | 0.27 | 25.59 | 17.03 |
| | | YellowC_F | F | 0.29 | 0.16 | 0.99 | No | 0.06 | 0.02 | 0.20 | 0.15 | 50.34 | 29.29 |
| | Ipswich 2018 | Blue_A_M | M | 14.80 | | 111.99 | No | 1.63 | | 6.57 | | 12.20 | |
| | | Blue_D_M | M | 1.60 | 0.53 | 3.49 | No | 0.39 | 0.23 | 0.84 | 0.34 | 54.75 | 4.31 |
| | | BlueA_F | F | 0.49 | 0.23 | 1.70 | No | 0.09 | 0.05 | 0.29 | 0.12 | 20.26 | 13.84 |
| | | RedB_M | M | 0.51 | 0.26 | 2.13 | No | 0.10 | 0.05 | 0.33 | 0.16 | 44.42 | 21.11 |
| | | RedC_M | M | 4.29 | 3.05 | 16.83 | No | 1.11 | 0.80 | 2.74 | 1.89 | 27.24 | 22.26 |
| | | YellowA_M | M | 3.57 | 2.08 | 11.47 | No | 0.74 | 0.47 | 1.64 | 1.11 | 24.78 | 21.14 |
| | Southwell 2016 | A_M | M | 1.12 | 0.52 | 3.45 | No | 0.28 | 0.23 | 0.64 | 0.40 | 37.35 | 19.28 |
| | | ArBr_F | F | 1.00 | 0.96 | 4.72 | No | 0.16 | 0.11 | 0.68 | 0.79 | 12.05 | 17.80 |
| | | ArCr_F | F | 0.41 | 0.13 | 0.99 | No | 0.11 | 0.07 | 0.32 | 0.07 | * | |
| | | BC_M | M | 1.48 | 0.83 | 4.98 | No | 0.40 | 0.28 | 0.96 | 0.61 | 33.86 | 9.15 |
| | | BCr_M | M | 3.61 | 2.08 | 10.18 | No | 0.65 | 0.33 | 2.04 | 0.90 | 50.09 | 36.78 |
| | | BrCr_F | F | 0.77 | 0.89 | 3.70 | No | 0.14 | 0.06 | 0.38 | 0.30 | 47.11 | 32.09 |

*The GPS tag failed to record GPS fixes on consecutive nights.

Table 4. 5. Average (mean ± SD) nightly home range estimates (hectares) for West European hedgehogs (*Erinaceus europaeus*) calculated using the Time Local Convex Hull (T-LoCoH) method at a) core range $UD_{50}$, 50% utilisation isopleth and b) home range $UD_{95}$, 95% utilisation isopleth and c) 100% MCP. Home range sizes are given for males and females across urban and rural areas, and both areas combined. Figures in parenthesis indicate the number of nightly home ranges used to calculate the average.

a) Core Range ($UD_{50}$)

| | Urban | Rural | Total |
|---|---|---|---|
| Male | 0.55 ± 0.47 (131) | 0.92 ± 0.86 (82) | 0.69 ± 0.67 (213) |
| Female | 0.21 ± 0.33 (94) | 0.43 ± 0.40 (130) | 0.34 ± 0.39 (224) |
| Total | 0.41 ± 0.45 (225) | 0.62 ± 0.66 (212) | |

b) Home Range ($UD_{95}$)

| | Urban | Rural | Total |
|---|---|---|---|
| Male | 1.55 ± 1.25 (131) | 2.60 ± 1.93 (82) | 1.95 ± 1.62 (213) |
| Female | 0.63 ± 0.80 (94) | 1.14 ± 0.88 (130) | 0.93 ± 0.89 (224) |
| Total | 1.17 ± 1.17 (225) | 1.70 ± 1.55 (212) | |

c) 100% MCP

| | Urban | Rural | Total |
|---|---|---|---|
| Male | 3.31± 3.64 (131) | 5.20 ± 4.28 (82) | 4.04 ± 4.00 (213) |
| Female | 1.08 ± 1.34 (94) | 2.02 ± 1.43 (130) | 1.63 ± 1.46 (224) |
| Total | 2.38 ± 3.11 (225) | 3.25 ± 3.27 (212) | |

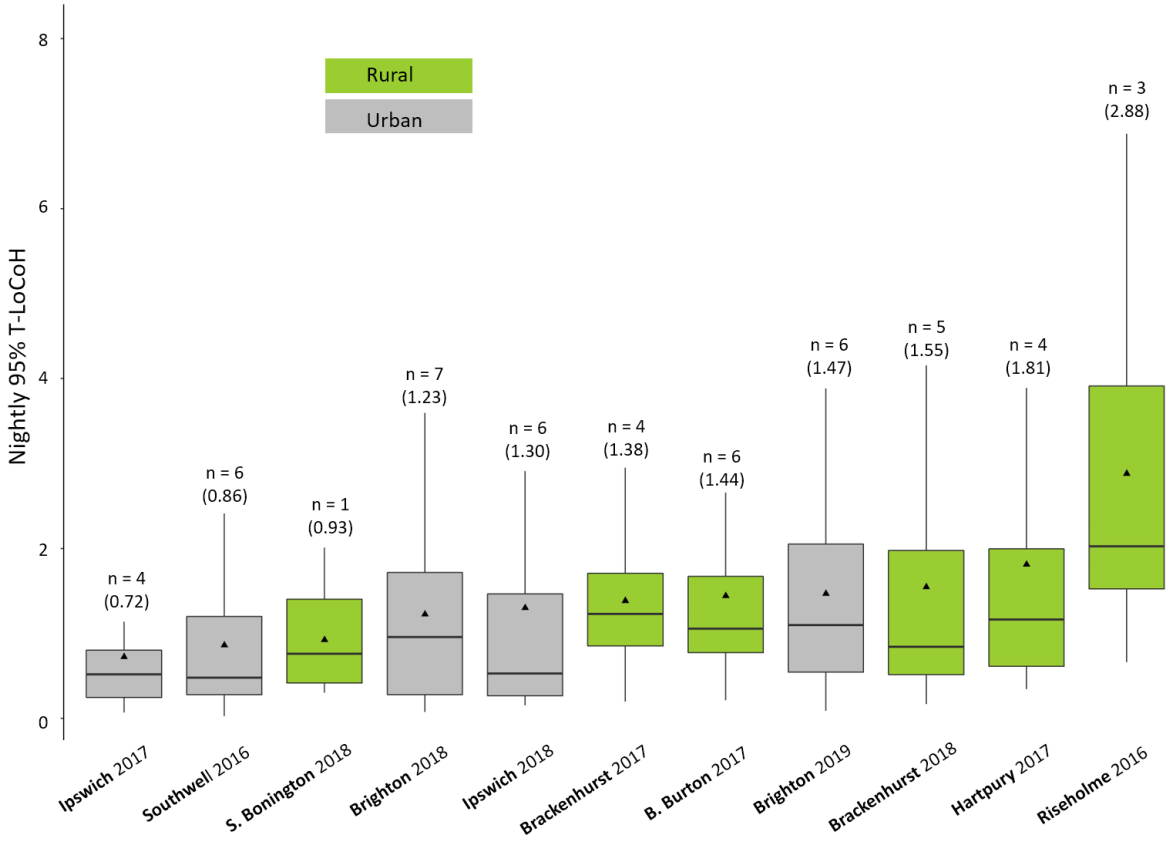



Figure 4. 2. Nightly home range of West European hedgehogs (*Erinaceus europaeus*) across urban (n=5) and rural (n=6) sites in England. The box represents the interquartile range and the whiskers the highest and lowest observation The median is shown by the horizontal line that divides the box and the mean by black triangles. The number of inviduals (n) used to estimate the home range size and the mean area obtained (hectares) are given above each boxplot.

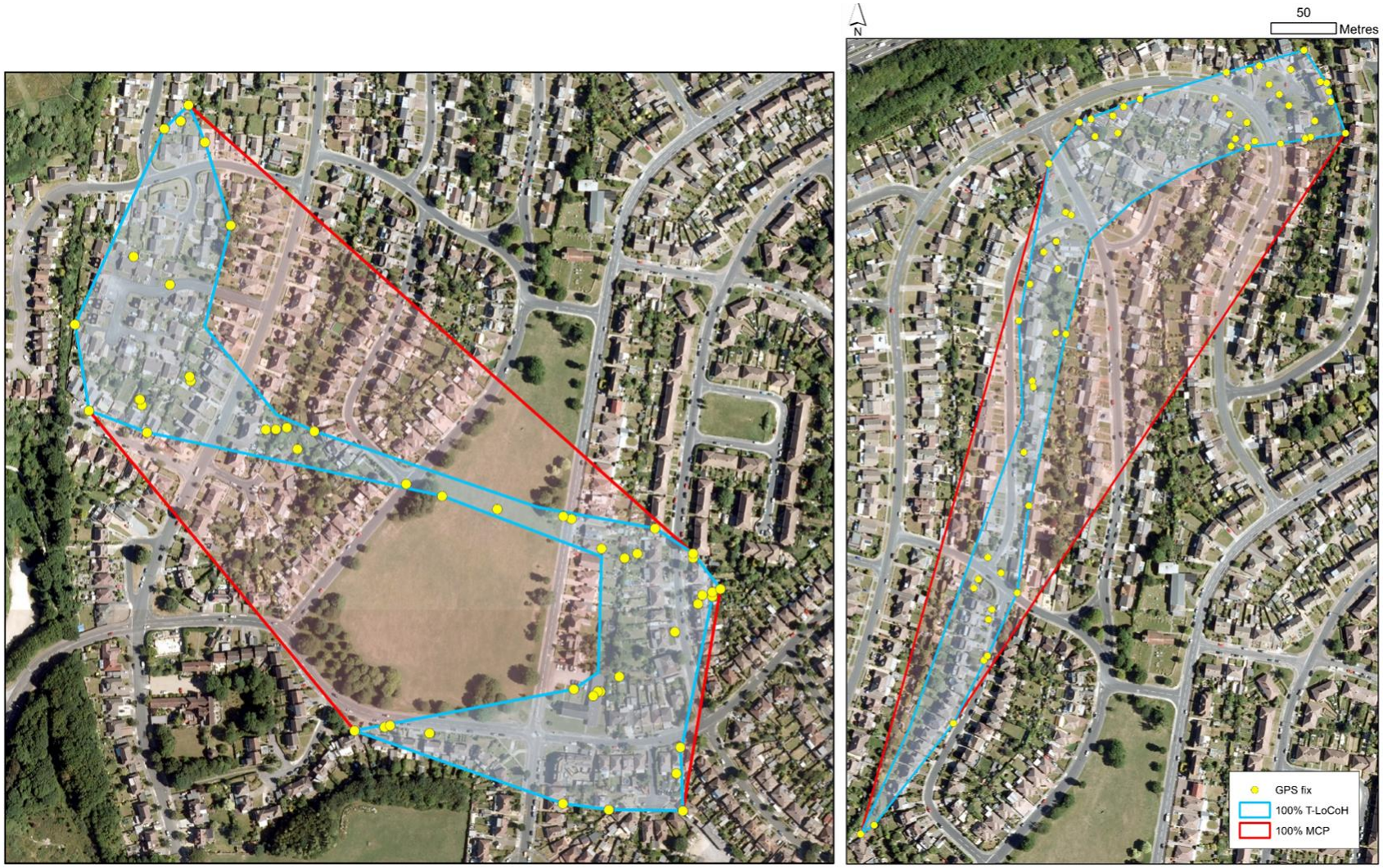



Figure 4. 3. Two examples of the home range area estimated by the MCP (red) and T-LoCoH (blue) methods when using all GPS fixes (100% isopleth). The area produced by the T-LoCoH method is smaller due to its ability to detect areas that are not visited by the individuals, providing a more realistic representation of space-use behaviour of animals.

Table 4. 6. Post-hoc Dunn's multiple comparisons test showing the differences in 95% T-LoCoH home range size across different study sites (n=11). Z and (p values) of each comparison are provided. Green and grey boxes belong to rural and urban sites, respectively. Significant p-values are shown in bold.* p≤ 0.05, ** p≤ 0.01, *** p≤ 0.001.

| Sites | Brackenhurst 2017 | Brackenhurst 2018 | Hartpury 2017 | Riseholme 2019 | Sutton Bonington 2018 | Brighton 2018 | Brighton 2019 | Ipswich 2018 | Ipswich 2017 | Southwell 2016 |
|---|---|---|---|---|---|---|---|---|---|---|
| Bishop Burton 2019 | 0.38 (-0.793) | -0.54 (-0.710) | 0.26 (0.839) | 3.75 **(0.001***)** | -1.19 (0.367) | -1.76 (0.161) | -0.11 (0.929) | -2.09 (0.088) | -3.36 **(0.004**)** | -3.17 **(0.006**)** |
| Brackenhurst 2017 | | -0.84 (-0.550) | -0.07 (0.942) | 3.06 **(0.008**)** | -1.37 (0.295) | -1.91 (0.118) | -0.47 (0.745) | -2.22 (0.069) | -3.39 **(0.004**)** | -3.17 **(0.007**)** |
| Brackenhurst 2018 | | | 0.69 (0.629) | 4.16 **(<0.001***)** | -0.89 (0.529) | -1.16 (0.375) | 0.43 (0.768) | -1.61 (0.190) | -2.91 **(0.012*)** | -2.60 **(0.025*)** |
| Hartpury 2017 | | | | 2.90 **(0.011*)** | -1.27 (0.332) | 1.64 (0.197) | 0.35 (0.799) | -1.99 (0.102) | -3.12 **(0.007**)** | -2.82 **(0.014*)** |
| Riseholme 2019 | | | | | -3.41 **(0.004**)** | 5.37 **(<0.001***)** | 3.85 **(0.001***)** | 5.13 **(<0.001***)** | 6.12 **(<0.001***)** | -6.38 **(<0.001***)** |
| Sutton Bonington 2018 | | | | | | -0.27 (0.847) | -1.13 (0.384) | 0.17 (0.895) | 1.09 (0.398) | 0.63 (0.650) |
| Brighton 2018 | | | | | | | 1.64 (0.191) | -0.71 (0.627) | -2.12 (0.085) | -1.63 (0.187) |
| Brighton 2019 | | | | | | | | -1.99 (0.106) | -3.27 **(0.005**)** | -3.06 **(0.008**)** |
| Ipswich 2018 | | | | | | | | | 1.27 (0.340) | -0.66 (0.634) |
| Ipswich 2017 | | | | | | | | | | 0.77 (0.593) |

Table 4. 7. Average (mean ± SD) number of GPS fixes used to estimate nightly home and core range size for West European hedgehogs (*Erinaceus europaeus*) using the Time Local Convex Hull (T-LoCoH) method. Averages are given for males and females across urban and rural areas, and both areas combined. Figures in parenthesis indicate the number of nightly home ranges used to calculate the average.

| | Urban | Rural | Total |
|---|---|---|---|
| Male | 45 ± 16 (131) | 66 ± 19 (82) | 53 ± 20 (213) |
| Female | 44 ± 14 (94) | 68 ± 21 (130) | 58 ± 22 (224) |
| Total | 44 ± 15 (225) | 67 ± 20 (212) | |

### *4.3.2 Predictors of daily home range size*

The best-fitting model to predict nightly home range size was model M12 (Table 4.9), which incorporated sex, landscape, and the proportion of gardens used. This model indicated a significant difference between males and females, where males have larger home ranges on a nightly basis, and between urban and rural landscapes, where home ranges in urban landscapes are smaller. The best model also showed a significant negative association between proportion of gardens used and home range size (Table 4.10), indicating that home ranges decrease as the proportion of gardens used increases.

Table 4. 8. Best-fitting generalised linear mixed models (GLMMs) to predict home range sizes of West European hedgehogs (*Erinaceus europaeus*) across urban and rural areas. AIC= Akaike's Information Criterion, $\Delta_i$ = delta AIC, $\omega$= AIC weighting.

| Model | Model formulation | AIC | $\Delta_i$ | $\omega$ |
|---|---|---|---|---|
| M12 | Sex + Landscape + Proportion of gardens used | 461 | 0 | 1 |
| M07 | Proportion of gardens used | 487 | 26 | 0 |
| M13 | Sex + Landscape + Average garden size accessed | 506 | 45 | 0 |
| M06 | Average garden size accessed | 513 | 52 | 0 |
| M11 | Sex + Landscape + Buildings density | 776 | 315 | 0 |
| M10 | Sex + Landscape + Number of gardens accessed | 778 | 317 | 0 |
| M03 | Buildings density | 790 | 329 | 0 |
| M05 | Number of gardens accessed | 812 | 351 | 0 |
| M08 | Sex + Landscape | 823 | 362 | 0 |
| M09 | Sex + Landscape + Daily precipitation (mm) + Minimum temperature | 824 | 363 | 0 |
| M01 | Sex | 831 | 370 | 0 |
| M02 | Landscape | 843 | 382 | 0 |
| M00 | Null | 845 | 384 | 0 |
| M04 | Daily precipitation (mm) + Minimum temperature | 846 | 385 | 0 |

Table 4. 9. Results of the best-fitting Gamma generalised linear mixed model to predict home range sizes of West European hedgehogs (*Erinaceus europaeus*) across urban and rural areas. Conditional $R^2$ was 0.75 which indicates the variance explained by the entire model, i.e., both fixed effects and random effects while the marginal $R^2$ was 0.62, indicating the variance explain only by the fixed effects. P-values of significant model factors are shown in bold. Individuals were modelled as a random factor. The reference category (intercept) relates to females and rural.

| Random effects | Variance | SD | | |
|---|---|---|---|---|
| Individual ID | 0.123 | 0.3507 | | |
| Residual | 0.2675 | 0.5172 | | |
| Fixed Effect | Estimate | SE | t value | Pr (>\|z\|) |
| *Intercept* | 0.9167 | 0.2244 | 4.09 | **<0.001** |
| $Sex_{(male)}$ | 0.6343 | 0.1886 | 3.36 | **<0.001** |
| $Habitat_{(urban)}$ | -0.9244 | 0.2081 | -4.44 | **<0.001** |
| Proportion of gardens used | -1.6397 | 0.1662 | -9.86 | **<0.001** |

### *4.3.3 Garden use*

On a nightly level (n=437), hedgehogs accessed 7.4 ± 8 gardens. The number of gardens accessed by rural hedgehogs (1.2 ± 1.9; range=0-9) was significantly lower than urban hedgehogs (13.1 ± 7.3; range=1-32) (U ($N_{urban}$=225, $N_{rural}$=212) = 926.5; p<0.05; Table 4.11). However, the number of gardens available was also significantly lower in rural (2.4 ± 3.5) than in urban (64 ± 74.6) landscapes (U ($N_{urban}$=225, $N_{rural}$=212) = 1162.5; p<0.05). When considering the proportion of gardens that were used from what was available in the landscape, rural hedgehogs used a higher proportion of gardens (65 ± 29%) than urban individuals (39 ± 26%) (U ($N_{urban}$=225, $N_{rural}$=212) = 14116.5; p<0.05). The proportion of gardens used by females (56 ± 29 %) was higher than for males (37± 26 %) (U ($N_{female}$=224, $N_{male}$=213) = 16483; p<0.05). The size of the gardens used by hedgehogs was significant lower in urban (0.04 ± 0.05 ha) than in the rural (0.06 ± 0.05ha) landscape (U ($N_{urban}$=225, $N_{rural}$=84) = 16315; p<0.05; Table 4.11). Furthermore, the size of the gardens used (0.0539 ± 0.0658 ha) were significant higher than those available (0.0531 ± 0.0688 ha) (Wilcoxon matched pairs signed rank test: V = 30209, p<0.05, n=319).

The proportion of gardens used also differed between sites (Kruskal-Wallis rank-sum test: H(9)= 84.821, p-value <0.05), with Southwell 2016 being the urban site with the

highest proportion of its gardens being used (48 ± 28 %) and Brighton 2019 having the smallest proportion of gardens used (23 ± 14 %) on a nightly basis (Table 4.12). In rural gardens, Brackenhurst 2017 had most of its gardens visited on a night (75 ± 26 %) while Sutton Bonington had the fewest proportion of gardens used (54 ± 22 %) but this data came from one individual limiting inference at this site.

On an individual level (n=52), rural hedgehogs used 88 ± 17% of the gardens available during their whole tracking period (range= 55-100%; Table 4.13), while the proportion of gardens used by urban individuals was almost half of that (43 ± 22 %; range= 11- 81%).

On a site level (n=11), the proportion of gardens used also varied between rural and urban landscapes, with rural sites having 80± 23 % of their gardens visited over a period of 9.4 ± 2.2 days, while only 23 ± 8 % of the gardens in urban sites were used over 9.6 ± 2.6 days (Table 4.14; $t = 5.31$, $df = 4.96$, $p<0.05$). Overall, Brighton 2018 was the urban site that had most of its gardens visited during the survey period (33%), while only 12% were visited in Ipswich 2017. Furthermore, a significant negative association was found between the percentage of gardens used at each site and buildings density (i.e., number of buildings within each 100% MCP) ($\beta=-0.35$, $p <0.05$).

Table 4. 10. Summary of the percentage and size of gardens available and visited by hedgehogs per night (n=437) in urban and rural landscapes. Values indicate the mean ± standard deviation; sizes are given in hectares (ha). M=male, F= female

| Landscape | Gardens available | | Gardens visited | | Percentage of gardens used within the availability | Sex | Gardens available | | Gardens visited | | Percentage of gardens used within the availability |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Number | Size (ha) | Number | Size (ha) | | | Number | Size (ha) | Number | Size (ha) | |
| Rural | 2.4 ± 3.5 | 0.06 ± 0.05 | 1.2 ± 1.9 | 0.06 ± 0.05 | 65 ± 29 | M | 2.6 ± 3.3 | 0.06 ± 0.08 | 1.0 ± 1.4 | 0.08 ± 0.09 | 52 ±25 |
| | | | | | | F | 2.2 ± 3.6 | 0.05 ± 0.02 | 1.4 ± 2.1 | 0.05 ± 0.02 | 73 ± 28 |
| Urban | 64 ± 74.6 | 0.05 ± 0.06 | 13.1 ± 7.3 | 0.04 ± 0.05 | 39 ±26 | M | 86.3 ± 87.6 | 0.06 ± 007 | 15.5 ± 8.1 | 0.05 ± 0.06 | 33 ± 25 |
| | | | | | | F | 32.9 ± 31.4 | 0.03 ± 0.01 | 9.9 ± 4.3 | 0.03 ± 0.01 | 47 ± 26 |

Table 4. 11. Post-hoc Dunn's multiple comparisons test showing the differences in percentages of garden use on a nightly basis across different study sites (n=10). Garden use for each site (mean percentage ± standard deviation), Z and (p-values) are provided. Green and grey boxes belong to rural and urban sites respectively. Significant p-values are shown in bold. * p≤ 0.05, ** p≤ 0.01, *** p≤ 0.001

| Sites | Brackenhurst 2017 (75 ± 26) | Brackenhurst 2018 (70 ± 30) | Hartpury 2017 (67 ± 0) | Sutton Bonington 2018 (54 ± 22) | Brighton 2018 (45 ± 28) | Brighton 2019 (23 ± 14) | Ipswich 2018 (46 ± 24) | Ipswich 2017 (40 ± 21) | Southwell 2016 (48 ± 28) |
|---|---|---|---|---|---|---|---|---|---|
| Bishop Burton 2019 (46 ± 25) | 2.71 **(0.018*)** | 2.19 (0.068) | 1.01 (0.502) | 0.61 (0.661) | -0.48 (0.726) | -3.41 **(0.003**)** | -0.19 (0.913) | -0.79 (0.620) | 0.04 (0.965) |
| Brackenhurst 2017 (75 ± 26) | | -0.69 (0.647) | -0.12 (0.923) | -1.45 (0.334) | -4.23 **(<0.001***)** | -7.54 **(<0.001***)** | -3.36 **(0.003**)** | -3.87 **(0.001***)** | -3.41 **(0.003**)** |
| Brackenhurst 2018 (70 ± 30) | | | 0.13 (0.939) | -1.01 (0.486) | -3.65 **(0.001***)** | -7.17 **(<0.001***)** | -2.80 **(0.014*)** | -3.36 **(0.003**)** | -2.80 **(0.015*)** |
| Hartpury 2017 (67 ± 0[1]) | | | | -0.63 (0.665) | 1.23 (0.425) | 2.36 **(0.046*)** | -1.11 (0.500) | -1.37 (0.367) | -1.03 (0.507) |
| Sutton Bonington 2018 (54 ± 22) | | | | | 1.05 (0.511) | 3.19 **(0.005*)** | 0.79 (0.638) | 1.25 (0.429) | 0.65 (0.664) |
| Brighton 2018 (45 ± 28) | | | | | | -4.51 **(<0.001***)** | 0.34 (0.827) | -0.51 (0.723) | 0.76 (0.633) |
| Brighton 2019 (23 ± 14) | | | | | | | 3.92 **(0.001***)** | 2.84 **(0.015*)** | 4.84 **(<0.001***)** |
| Ipswich 2018 (46 ± 24) | | | | | | | | 0.71 (0.650) | 0.29 (0.842) |
| Ipswich 2017 (40 ± 21) | | | | | | | | | 1.05 (0.526) |

[1]Only 2 gardens visited on 2 nights

Table 4. 12. Average and proportion of gardens used by each individual in relation to habitat available (100% MP). Habitat available was calculated on three different scales: nightly level, individual level and site level. The table includes the number of gardens, size (hectares) and percentage of gardens each individual visited. Max= maximum number of gardens visited on a single night. SD= Standard Deviation.

| Landscape | Site | Hedgehog ID | Sex | Gardens used on nightly level | | | | | | | Percentage of gardens used on the individual level | Percentage of gardens used on the site level |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Number of gardens | | | Garden size (ha) | | Percentage of gardens | | | |
| | | | | Max | Mean | SD | Mean | SD | Mean | SD | | |
| Rural | Bishop Burton 2019 | BlueA_M | M | 3 | 2.4 | 0.5 | 0.045 | 0.010 | 36 | 6 | 55 | 50 |
| | | BlueB_F | F | 0 | | | | | | | | |
| | | BlueC_M | M | 4 | 2.6 | 0.8 | 0.062 | 0.011 | 40 | 18 | 67 | 50 |
| | | BlueD_F | F | 0 | | | | | | | | |
| | | BlueE_F | F | 1 | 1.0 | | 0.040 | | 100 | | 100 | 8 |
| | | BlueG_M | M | 1 | 1.0 | | 0.040 | | 100 | | 100 | 8 |
| | Brackenhurst 2017 | BlackDD_F | F | 6 | 4.4 | 1.1 | 0.052 | 0.003 | 88 | 11 | 100 | 86 |
| | | BlackEE_F | F | 5 | 2.4 | 1.5 | 0.058 | 0.013 | 56 | 28 | 100 | 86 |
| | | BlackHH_F | F | 3 | 1.5 | 0.8 | 0.052 | 0.005 | 77 | 26 | 80 | 57 |
| | | BlueCC_M | M | 1 | 1.0 | | 0.074 | | 100 | | 100 | 14 |
| | Brackenhurst 2018 | BlackDD_F | F | 6 | 3.4 | 1.9 | 0.056 | 0.005 | 93 | 17 | 100 | 40 |
| | | BlackEE_F | F | 4 | 1.8 | 1.1 | 0.056 | 0.037 | 64 | 34 | 100 | 53 |
| | | BlueAA_F | F | 0 | | | | | | | | |
| | | BlueCC_M | M | 3 | 2.8 | 0.5 | 0.053 | 0.009 | 75 | 29 | 86 | 40 |
| | | YellowAA_M | M | 5 | 3.1 | 1.1 | 0.071 | 0.018 | 48 | 24 | 60 | 60 |
| | Hartpury 2017 | BH_M | M | 2 | 2.0 | 0.0 | 0.391 | 0.097 | 67 | 0 | 100 | 100 |
| | | RA_M | M | 0 | | | | | | | | |
| | | RB_F | F | 0 | | | | | | | | |
| | | RH_F | F | 0 | | | | | | | | |
| | Riseholme 2019 | BlueA_M | M | 0 | | | | | | | | |
| | | BlueB_F | F | 0 | | | | | | | | |
| | | BlueC_F | F | 0 | | | | | | | | |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Sutton Bonington 2018 | YellowA_F | F | 9 | 6.4 | 1.9 | 0.053 | 0.005 | 53 | 22 | 88 | 88 |
| Urban | Brighton 2018 | Blue_E_F | F | 17 | 12.2 | 3.4 | 0.037 | 0.006 | 65 | 18 | 64 | 4 |
| | | BlueA_M | M | 28 | 23.0 | 4.0 | 0.036 | 0.006 | 15 | 8 | 19 | 14 |
| | | BlueC_M | M | 31 | 21.1 | 6.3 | 0.026 | 0.003 | 31 | 17 | 29 | 14 |
| | | RedC_F | F | 8 | 6.1 | 1.4 | 0.045 | 0.007 | 84 | 14 | 73 | 1 |
| | | RedD_F | F | 13 | 9.7 | 2.1 | 0.034 | 0.004 | 80 | 10 | 81 | 2 |
| | | YellowA_M | M | 27 | 17.9 | 6.4 | 0.036 | 0.004 | 26 | 13 | 34 | 10 |
| | | YellowC_M | M | 30 | 21.2 | 5.7 | 0.036 | 0.003 | 35 | 5 | 70 | 7 |
| | Brighton 2019 | BlackA_M | M | 17 | 12.1 | 4.5 | 0.023 | 0.004 | 27 | 16 | 35 | 6 |
| | | BlackC_F | F | 20 | 11.6 | 4.1 | 0.023 | 0.003 | 23 | 12 | 33 | 9 |
| | | BlackD_M | M | 23 | 15.4 | 4.0 | 0.020 | 0.003 | 24 | 11 | 30 | 11 |
| | | BlueA_F | F | 15 | 13.1 | 1.4 | 0.032 | 0.002 | 38 | 5 | 64 | 4 |
| | | RedA_M | M | 16 | 12.2 | 2.6 | 0.033 | 0.007 | 11 | 11 | 15 | 8 |
| | | RedC_F | F | 11 | 6.9 | 3.1 | 0.030 | 0.008 | 8 | 4 | 11 | 4 |
| | Ipswich 2017 | BlueF_F | F | 16 | 12.5 | 2.3 | 0.012 | 0.003 | 25 | 8 | 40 | 9 |
| | | RedC_M | M | 31 | 17.4 | 9.4 | 0.020 | 0.003 | 20 | 9 | 21 | 11 |
| | | RedH_F | F | 25 | 17.2 | 4.8 | 0.021 | 0.004 | 42 | 12 | 42 | 8 |
| | | YellowC_F | F | 17 | 10.3 | 4.2 | 0.016 | 0.002 | 64 | 15 | 48 | 4 |
| | Ipswich 2018 | Blue_A_M | M | 27 | 27.0 | | 0.090 | | 11 | | 15 | 10 |
| | | Blue_D_M | M | 32 | 23.3 | 6.2 | 0.021 | 0.001 | 43 | 7 | 57 | 4 |
| | | BlueA_F | F | 14 | 11.2 | 2.4 | 0.022 | 0.003 | 57 | 20 | 80 | 3 |
| | | RedB_M | M | 16 | 10.7 | 3.6 | 0.031 | 0.002 | 69 | 16 | 66 | 3 |
| | | RedC_M | M | 32 | 23.2 | 5.8 | 0.025 | 0.004 | 25 | 17 | 25 | 9 |
| | | YellowA_M | M | 32 | 24.8 | 7.9 | 0.024 | 0.002 | 24 | 7 | 34 | 9 |
| | Southwell 2016 | A_M | M | 7 | 4.3 | 1.3 | 0.184 | 0.044 | 70 | 25 | 72 | 6 |
| | | ArBr_F | F | 7 | 5.4 | 1.3 | 0.039 | 0.013 | 41 | 27 | 29 | 10 |
| | | ArCr_F | F | 7 | 5.8 | 1.0 | 0.053 | 0.008 | 44 | 13 | 41 | 5 |
| | | BC_M | M | 11 | 6.1 | 2.5 | 0.197 | 0.018 | 61 | 19 | 58 | 7 |
| | | BCr_M | M | 14 | 6.9 | 4.0 | 0.033 | 0.009 | 22 | 32 | 22 | 16 |
| | | BrCr_F | F | 8 | 5.9 | 1.5 | 0.030 | 0.006 | 39 | 14 | 38 | 8 |

Table 4. 13. Summary of the gardens available and accessed in each study area during the whole survey period. SD= Standard Deviation. *Only one garden was found in Riseholme 2019 and it was not used by any hedgehog.

| Landscape | Site | Garden size available | | Garden size used | | Percentage of gardens used |
|---|---|---|---|---|---|---|
| | | Mean | SD | Mean | SD | |
| Rural | Brackenhurst 2017 | 0.0437 | 0.0242 | 0.0532 | 0.0103 | 100 |
| | Hartpury 2017 | 0.4010 | 0.1130 | 0.3945 | 0.1004 | 100 |
| | Brackenhurst 2018 | 0.0702 | 0.0551 | 0.0602 | 0.0195 | 63 |
| | Sutton Bonington 2018 | 0.0498 | 0.0136 | 0.0530 | 0.0140 | 88 |
| | Bishop Burton 2019 | 0.0231 | 0.0268 | 0.0585 | 0.0251 | 50 |
| | Riseholme 2019* | 0.0131 | | | | |
| Urban | Southwell 2016 | 0.0286 | 0.0412 | 0.1034 | 0.1035 | 27 |
| | Ipswich 2017 | 0.0086 | 0.0069 | 0.0173 | 0.0081 | 12 |
| | Brighton 2018 | 0.0194 | 0.0137 | 0.0348 | 0.0132 | 33 |
| | Ipswich 2018 | 0.0251 | 0.0333 | 0.0313 | 0.0295 | 22 |
| | Brighton 2019 | 0.0202 | 0.0129 | 0.0259 | 0.0105 | 21 |

### *4.3.4 Nightly overlap*

Overall, the percentage of nightly home range ($UD_{95}$) overlap was low (33.8 ± 25.5 %). However, the percentage of nightly overlap differed between landscapes: overlap was significantly higher in rural (38.2 ± 25.9 %) compared to urban landscapes (29.1 ± 24.2 %) (U ($N_{urban}$=186, $N_{rural}$=195) = 21967; $p<0.05$). No significant difference of nightly overlap was found between males (32.1 ± 24.8 %) and females (35.5 ± 26 %) (U ($N_{urban}$=186, $N_{rural}$=195) = 19452; p=0.23).

## 4.4 Discussion

We used high-frequency data to study space-use behaviour of West European hedgehogs in urban and rural habitats across England. Our study suggests that, on a small spatial and temporal scale, small mammals do not encounter barriers to movement in urban areas, as they can visit different parts of cities/towns on consecutive nights. Our findings showed differences in home range size between male and female hedgehogs, and urban and rural landscapes, where the largest home ranges were displayed by males in rural areas. However, animal movement could be influenced by the distribution and availability of vital resources. Indeed, in areas with a low proportion of gardens used, hedgehogs ranged greater distances, probably to find the much-needed resources found in gardens. These findings highlight the importance of gardens to wildlife and, therefore, urban planning and development should ensure not only that green spaces are available but that they are accessible.

This study is the first to calculate nightly home ranges of hedgehogs using T-LoCoH and, as such, the estimates cannot be compared to previous studies. Indeed, when looking at the literature, there is no agreement on the appropriate sampling period to use when tracking hedgehogs (Table 4.15). Here, home ranges are provided with a sampling period (i.e., nightly) that can easily be replicated in future studies to allow comparison and a methodology that provides great advantages in the analysis of high-frequency data.

Nevertheless, nightly 100% MCP was also estimated to allow comparison and showed that the nightly 100% MCP for urban males and females are similar to areas reported in Berlin and Bristol (Dowding et al., 2010; Barthel, 2019; Table 4.15). Furthermore, the 100% MCP estimated for males during their whole tracking period in urban landscapes (21 ± 27; n=16) are similar, but slightly higher, to the results reported by Braaker et al.

(2014) in Switzerland (17 ± 3 SE, n=40). The difference in the areas could be because Braaker et al. (2014) tracked hedgehogs for 1-6 nights, compared to 5-15 nights in this study, and larger areas might be a result of longer tracking periods. Furthermore, the 100% MCP of rural individuals found here (17.4 ± 22.9; n=1) are in accordance with previous research (21.2 ± 4.7 ha, Glasby and Yarnell, 2013; 21.9± 5 ha, Pettett et al., 2017b). Therefore, the agreement in the home range sizes found with previous research using the MCP method is encouraging for the results obtained in the T-LoCoH estimations.

Regarding the methodology used here, home ranges were calculated using the T-LoCoH method to take advantage of the high-frequency data and to integrate time with space. Although the T-LoCoH method has been applied to study space use of large mammals (cheetahs *Acinonyx jubatus*, Van Der Weyde et al., 2017; orangutans *Pongo pygmaeus wurmbii*, Tarszisz et al., 2018; black rhinos *Diceros bicornis*, Seidel et al., 2019), and marine species (grey seals *Halichoerus grypus*, Baker et al., 2015; Atlantic sturgeons *Acipenser oxyrinchus oxyrinchus*, Whitmore and Litvak, 2018), it has not been used to study space use of small or medium mammals, neither has it been implemented in urban landscapes (but see Dürr and Ward (2014) that evaluated the home range of domestic dogs in Australia).

Most published information about home ranges of hedgehogs is based on radio-tracking data using the MCP method, a method that, when used to calculate home range, typically overestimates the area used by animals (Getz and Wilmers, 2004; Getz et al., 2007). Indeed, the T-LoCoH method produced smaller home ranges in comparison to MCP (Figure 4.3). However, the ability of the T-LoCoH method to identify areas that are not used by individuals has allowed a more accurate estimation of home ranges and therefore, better representation of space-use behaviours.

Table 4. 14. Summary of the home-range (ha, mean ± SD) of West European hedgehogs (*Erinaceus europaeus*) from different studies. The summary includes the data type, the number of individuals (n), source, country, landscape type (urban/rural), time scale and the methods used in the calculations. HR = home range size, SD=Standard Deviation, SE=Standard Error, n= number of individuals, RT=radio tracking, GPS= Global Positioning System, MCP=Minimum Convex Polygon, UD=Utilization Distribution, LoCoH= Local Convex Hull, T-LoCoH=Time Local Convex Hull; '–' Indicates that sample size was not reported.

| Landscape | Sex | HR ± SD | Data | n | Source | Country | Time scale | Method |
|---|---|---|---|---|---|---|---|---|
| Rural | F | 9.8 ± 2.2 | RT | 6 | Reeve 1982 | United Kingdom | Annual | MCP (100% UD) |
| | M | 32.3 ± 8.9 | | 6 | | | | |
| | F | 96 ± 24 | RT | 4 | Riber 2006 | Denmark | May and July | MCP (100% UD) |
| | M | 26 ± 15 | | 4 | | | | |
| | F | 4.4 ± 1 (SE) | RT | 17 | Hof 2009 | United Kingdom | May-July | MCP (95% UD) |
| | M | 24.9 ± 3.7 (SE) | | 16 | | | | |
| | F+M | 18.3 ± 3.7 | RT | 9 | Glasby and Yarnell, 2013 | United Kingdom | 5 nights | MCP (100% UD) |
| | | 21.2 ± 4.7 | GPS | | | | | |
| | F | 16.5 ± 0.49 (SE) | RT | 3 | Haigh, O'Riordan and Butler, 2013 | Ireland | Annual | MCP (100% UD) |
| | M | 56.0 ± 0.67 (SE) | | 4 | | | | |
| | F | 12.7 ±0.4 | GPS | 2 | Rodriguez Recio et al., 2013 | New Zealand | 4-5 nights (Summer) | LoCoH (100% UD) |
| | M | 45.3 ± 5.9 | | 13 | | | | |
| | F | 12.4 ± 2.7 | RT | 15 | Pettett et al., 2017b | United Kingdom | Annual | MCP (100% UD) |
| | M | 21.6 ± 5.8 | | 17 | | | | |
| | F | 1.1 ± 0.9 | GPS | 14 | This study | United Kingdom | Nightly | LoCoH (95% UD) |
| | M | 2.6 ± 1.9 | | 9 | | | | |
| Urban | F | 0.77 ± 0.40 | RT | 19 | Dowding et al., 2010 | United Kingdom | Nightly | MCP (100% UD) |
| | M | 2.87 ± 1.74 | | 19 | | | | |
| | F | 55.2 ± 17.1 | RT | 3 | Rautio, Valtonen and Kunnasranta, 2013 | Finland | May-June | MCP (100% UD) |
| | M | 97.9 ± 6.1 | | 4 | | | | |
| | M | 17.3 ± 3.0 (SE) | GPS | 40 | Braaker et al., 2014 | Switzerland | 1-6 nights | MCP (100% UD) |
| | F | 2.5 | GPS | - | Barthel, 2019 | Germany | Nightly | MCP (95% UD) |
| | M | 4.7 | | - | | | | |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | F<br>M | 1.4 ± 0.9<br>3.2 ± 3.9 | RT | 8<br>14 | Rasmussen et al., 2019 | Denmark | Autumn, Spring | MCP (95% UD) |
| | F<br>M | 0.6 ± 0.8<br>1.6 ± 1.3 | GPS | 13<br>16 | This study | United Kingdom | Nightly | LoCoH (95% UD) |

### *4.4.1 Predictors of daily home range size*

The best fitting model to predict hedgehog nightly HR included sex of individuals, type of landscape and proportion of gardens. The average home range of males was typically twice as large as that of females. This finding is in accordance with previous studies carried out over longer temporal scales and based on different home range calculations (Riber, 2006; Dowding et al., 2010; Haigh, O'Riordan and Butler, 2013; Rautio, Valtonen and Kunnasranta, 2013; Rodriguez Recio et al., 2013; Pettett et al., 2017b). The larger home ranges of males are explained by their promiscuous mating behaviour, as males range further and cover larger areas to mate with as many females as possible and maximise fitness (Morris, 2018). On the other hand, females tend to have smaller ranges, mainly focusing their activities on searching for food to build up fat reserves for reproduction (Haigh, O'Riordan and Butler, 2013; Rautio, Valtonen and Kunnasranta, 2013). Nightly areas ranged in rural landscapes were 1.5x those recorded in urban areas. The difference in space-use between individuals of different sex and in different landscapes has been widely reported in the literature across other urban mammal species such as coyotes, bobcats and squirrels (e.g., Riley et al., 2003; Grubbs and Krausman, 2009; Mäkeläinen et al., 2016), where differences in reproductive tactics between males and females, and the distribution of resources in the landscape, have been suggested as the reasons behind this movement behaviour.

### *4.4.2 Garden use*

The proportion of gardens used had a negative relationship with home range size: home ranges were smaller in areas where hedgehogs used most of the gardens available. This suggests that gardens provide vital resources for hedgehogs, and in the lack of these resources, individuals must range further and cover larger areas to meet their nightly requirements.

The difference in the number of gardens used by males and females supports previous studies that advocate that hedgehog behaviour is mainly driven by different reproductive tactics (Reeve, 1994; Morris, 2006), where females will focus on building fat reserves, exploiting the resources available more intensively and, therefore, visiting a higher proportion of gardens. In comparison, the proportion of gardens used by males was lower, but they showed larger home ranges, with further distances recorded on single nights, covering large distances at higher speeds and, therefore, missing gardens

available in their habitat. Such behaviour can again be explained by the mating behaviour of the males, aiming to mate with as many females as possible (Reeve, 1994; Morris, 2006) and, therefore, not dedicating as much time to explore the landscape and exploit the resources available as females do.

The significantly higher proportion of gardens used in rural landscapes on a nightly basis suggests that in this type of landscape, where a limited number of gardens are available, gardens are a valuable resource for hedgehogs. If gardens in rural landscapes are indeed resource-rich areas, hedgehogs with access to a handful of gardens may be forced to forage in alternative, less productive habitats, once the garden patch has been exploited, such as field margins and amenity grassland and, as a result, range more widely in rural landscapes, as found here. However, habitat selection studies in urban areas might be needed to better understand the importance of gardens in relation to other habitats available.

As there was no data regarding how permeable to wildlife the boundaries of each garden was (i.e., whether gardens had impermeable boundaries such as brick walls, or more permeable such as wooden or living fences), identifying whether the gardens that were never accessed were indeed inaccessible to hedgehogs, was not possible. Therefore, it cannot be concluded whether access to gardens is limiting hedgehog movements. However, the study found that the presence of gardens influences space-use behaviour of hedgehogs. In urban areas, gardens constitute a significant proportion of green space (Loram et al., 2007) and provide vital resources for many species (Goddard, Dougill and Benton, 2010). For example, gardens represent good habitats for many invertebrates (Jones and Leather, 2012) and, therefore, provide foraging ground for higher trophic levels such as badgers (Cresswell and Harris, 1988), possums (Adams et al., 2013), racoons (Hoffmann and Gottschang, 1977) and hedgehogs (Braaker et al., 2014). Gardens also provide daytime cover (foxes; Harris, 1977) and nesting sites for wildlife (hedgehogs; Braaker et al., 2014). Despite the findings showing that gardens influence space-use behaviour of hedgehog, the reasons behind it are largely unknown. For example, it is not known whether, in the study areas, gardens were only being used as a foraging ground or, as suggested in other urban movement studies (Barthel, 2019), whether they were also being used as travelling corridors, connecting different patches of cities/towns. With recent advances in movement ecology, high-frequency data, as

obtained in this study, could be used to understand what is motivating animals to move (e.g., finding food, dispersing) in relation to habitat characteristics and, therefore, obtain a better insight into the importance of gardens, not only for hedgehogs but for any small mammals moving through the urban landscape.

### *4.4.3 Nightly overlap*

Analysis of nightly home range overlap found that, on a small scale, from one night to another, hedgehogs showed a low percentage (33%) of home range overlap. Such low levels may have resulted from using only a small proportion of the home range on consecutive nights (i.e., nesting areas) while shifting the remainder of the home ranges used, visiting other different areas on consecutive nights in search of resources. Hedgehogs are known to re-use the same nests on consecutive nights (Rast, Barthel and Berger, 2019), so some degree of overlap is expected. However, this study found a higher level of overlap in the rural (38%) than in the urban (29%) landscape. Higher levels of overlap found in the rural landscape result by individuals re-using the same areas on consecutive nights, with little home range shift. Such behaviour could be due to the distribution of resources, as organisms are constantly re-using the same areas (e.g., rural gardens) to obtain the resources they need, or due to movement limitations if the animal movement is restricted to the same areas due to the presence of barriers such as roads or other anthropogenic infrastructures. Based on the larger home ranges recorded in rural landscapes, the higher level of overlap is unlikely due to movement restriction and more likely due to the distribution of resources, as suggested by the high proportion of gardens used (80%) in this landscape despite their low availability. The lower levels of overlap in the urban landscape suggest that individuals are relying on different areas of the landscape to obtain their resources and that their movement is not being restricted. Indeed, urban hedgehogs visited up to 32 gardens per night, suggesting not only that they rely on a good number of gardens to obtain the needed resources, but that they can freely move between them. On a large spatial scale, urbanisation has been shown to restrict animal movements due to the presence of physical barriers (Rondinini and Doncaster, 2002; Atwood, Weeks and Gehring, 2004; Ellington and Gehrt, 2019). In this study, on a small temporal and spatial scale, the low nightly overlap (29%) suggested that no barriers to movement were apparent.

Despite the findings suggesting that in urban areas, on a small spatial and temporal scale, there were no barriers stopping individuals from moving and exploring different areas of the landscape, not all gardens available were used and the proportion of gardens used decreased with increased urbanisation (i.e., buildings density). On a nightly basis, only 39% of available gardens in the urban landscape were used by hedgehogs and, on a site level, Brighton 2018 had the highest proportion of gardens used (Table 4.13), which accounted for only 33% of gardens. These low percentages suggest that, despite individuals exploring different areas of the landscape, hedgehogs focus their activities on only a small proportion of gardens; and this could be the reason influencing small home ranges of urban individuals. Hedgehogs focus their activities on gardens probably as these provide the resources they need in order to maximise the amount of resources obtained, whilst reducing travel costs. However, these findings provide only a snapshot (i.e., 10 days) of what hedgehogs are doing. Long-term studies are needed to assess whether, when a home range asymptote has been reached (e.g., annual home range), the proportion of gardens used also increases as suggested by Gazzard and Baker (2020) who found that, on average, 46.6% of the gardens in Reading (UK) are used over a month while active during autumn and spring. Long-term movement studies would provide more details of how accessible the landscape is for wildlife, and if this is having an impact on the long-term space-use of animals, or if habitat permeability drives only short-term space-use behaviour of hedgehogs.

### *4.4.4 Recommendations*

Understanding animal movements and space-use is needed to inform conservation management (Allen and Singh, 2016). This study found that movement and space-use behaviour across urban and rural landscapes is influenced not only by biotic (i.e., sex, weight) but abiotic features: gardens are vital habitats for the species. As promoting landscape connectivity has become a conservation goal in human-dominated landscapes to maintain wildlife populations and mitigate rates of habitat loss and fragmentation (Bennett, Crooks and Sanjayan, 2010), urban planning should include the management of gardens with wildlife in mind, not only to ensure that good-quality well-connected habitats are present in the urban landscape, but that these habitats are accessible to wildlife (Baycan-Levent et al., 2002; Vargas-Hernández, Pallagst and Zdunek-Wielgołaska, 2018). This is of vital importance as growing rates of urbanisation

reduce the availability of green areas (Baycan-Levent et al., 2002), and urbanisation and densification of cities are expected to continue increasing (United Nations, 2018).

This study did not have data to conclude whether the lack of accessibility to gardens was limiting hedgehog movements. What is clear is that gardens are widely utilised and any conservation action such as Gardening for Wildlife encouraging homeowners to make their gardens wildlife-friendly (RSPB, 2020), and the 'hedgehog highway' campaign to encourage access to gardens by making fences more permeable (PTES and BHPS, 2020), will likely be beneficial for wildlife (Hof and Bright, 2009). Such actions are needed as, despite some mammalian species having higher densities in cities/towns (Herr, Schley and Roper, 2009; Prange et al., 2003; Bateman and Fleming, 2012), ensuring that resources are accessible is vital to maintain stable populations of urban species in the long-term.

Finally, season is known to influence the movement and space-use behaviour of hedgehogs (Riber, 2006; Dowding et al., 2010; Haigh, O'Riordan and Butler, 2013; Rasmussen et al., 2019; Rautio, Valtonen and Kunnasranta, 2013; Rodriguez Recio et al., 2013), and to have an effect on the sex of individuals: males have larger home ranges during the mating season while females have larger home ranges during pre-hibernation (Rautio, Valtonen and Kunnasranta, 2013). However, due to a lack of individuals tracked during August-September in urban areas, the effect of season on space-use and movement of hedgehogs was not investigated. Further research should account for differences of space-use throughout the year to better understand the seasonal space requirement needs of the species.

## 4.5 Conclusion

High-frequency GPS movement data has been used to study the space-use behaviour of hedgehogs in urban and rural habitats. This study found that, on a small spatial and temporal scale, small mammals do not encounter barriers to movement in the urban landscape, as individuals can visit different areas on consecutive nights. However, access to vital resources plays an important role in shaping space-use behaviour on a nightly basis. Gardens are important habitats, not only for hedgehogs but many other species and, therefore, urban planning should ensure that these habitats are accessible to wildlife. These actions will create a well-connected network of suitable habitats and

promote animal movement and habitat connectivity, encouraging the presence of wildlife in urban landscapes.

# CHAPTER FIVE

# Movement behaviour and habitat selection of hedgehogs in urban and rural landscapes

## 5.1 Introduction

Movement of organisms is vital in many ecological and evolutionary processes (Nathan and Giuggioli, 2013). In the short-term, animal movement is usually associated with searches for critical resources (e.g., food, shelter and mating opportunities), and avoiding risks such as predation, where long-term fitness implications include the avoidance of inbreeding (Holyoak et al., 2008; Nathan et al., 2008). Due to the implications of movement decisions for individuals, populations and communities, there is a growing interest in understanding animal movement (Holyoak et al., 2008).

Movement decisions are influenced by the information animals receive while navigating through the landscape, which, in turn, affects animal space-use (Moorcroft and Barnett, 2008; Forester, Im and Rathouz, 2009; Moorcroft, 2012; Van Moorter et al., 2016; Patterson et al., 2017). Understanding how individuals move and respond to their environment is especially important in human-dominated areas, where urbanisation can alter the landscape in ways that might require animals to modify their movement in response to infrastructure (e.g., roads) or due to the modification of the distribution of resources, i.e., high-quality patches separated by less favourable habitats (Beyer et al., 2016; Parris, 2016; Karelus et al., 2017; James, 2018). This movement-modification might reduce the ability of animals to forage optimally by potentially incurring energetic and demographic costs (Sawyer et al., 2013).

The observed movement patterns of an individual are determined both by internal components (i.e., behavioural state, motion and navigation capacities) and external environmental factors such as weather, habitat and the presence of other individuals (Nathan et al., 2008). Although many of these extrinsic factors can be measured, internal factors, such as an animal's behavioural state, are often difficult to quantify, especially for species that are nocturnal, elusive, and difficult to observe (Karelus et al., 2019). Based on the motivation of animals to move (e.g., finding food, mates, nesting materials), individuals may select different habitats to meet their requirements

(Moorcroft and Barnett, 2008; Forester, Im and Rathouz, 2009; Moorcroft, 2012; Van Moorter et al., 2016). Taking into account movement behaviour is needed not only to make meaningful inferences about which habitats individuals are selecting and the importance of different habitat types for species (Cozzi et al., 2016; Abrahms et al., 2017), but also to understand the motives that lead an animal's decision to select a specific habitat or area (Karelus et al., 2019; Beumer et al., 2020).

The study of animal behaviour from the observed movement patterns of animals and how different features of the landscape influence such behaviours, has recently been facilitated by Hidden Markov Models (HMMs). HMMs have been applied to study animal movement behaviour to identify habitats needed for foraging and denning, and features of the landscape that facilitate movement between habitat patches (e.g., bettongs *Bettongia gaimardi*; Gardiner et al., 2019). HMMs are also used to understand changes in seasonal movement behaviours of wildlife (e.g., Karelus et al., 2019; Beumer et al., 2020).

Recent studies of the West European hedgehog have shown that individual movement and space-use is influenced by landscape (rural versus urban; Chapter 4), the proportion of gardens that individuals use (Chapter 4), the presence of built-up areas (Pettett et al., 2017b), the presence of roads (Rondinini and Doncaster, 2002) and the sex of the individual (Riber, 2006; Haigh, O'Riordan and Butler, 2013).

To date, many studies have shown that hedgehogs exhibit habitat preferences (e.g., Riber, 2006; Haigh, O'Riordan and Butler, 2013; Rodriguez Recio et al., 2013; Pettett et al., 2017b), but it is not known how these habitats are used, or for what purpose. For example, previous studies have found that gardens are important for hedgehogs, as this habitat is strongly selected both in urban and rural landscapes (Dowding et al., 2010; Haigh, O'Riordan and Butler, 2013; Braaker et al., 2014; Pettett et al., 2017b). However, whether the selection of gardens is due to food resources, safe foraging habitats, paths of least resistance through the landscape, or a combination of these factors has yet to be investigated. As foraging and dispersal are essential parts of hedgehog ecology (Wroot, 1984; Reeve, 1981; Morris, 2018), identifying which habitats facilitate these behaviours is important for understanding how landscape affects the survival of individuals, connectivity of populations, and persistence of the species across different landscapes. This is urgently needed as, despite urban gardens covering up to 22-36% of

the total urban land cover (Loram et al., 2007; Baldock et al., 2019), they are usually fragmented in small areas (~190m$^2$, Davies et al., 2009) and subject to different management practices (Politi Bertoncini et al., 2012). This level of fragmentation can influence hedgehog persistence across the wider urban landscape, especially if gardens are not suitable or accessible for the species. Furthermore, with the current increase in the human population, and subsequent urbanisation, pressure on these habitats could increase, with a consequent reduction in its availability to wildlife. For example, when evaluating the availability of green space per inhabitants in metropoles and big cities, research indicates that green space availability is decreasing with the growing human population (Baycan-Levent et al., 2002).

In this study, high-resolution Global Positioning System (GPS) location data was used to: (1) identify the behavioural states underlying the observed movement patterns of hedgehogs using HMMs; (2) incorporate these behavioural states to discern habitat selection in urban and rural landscapes, across males and females.

## 5.2 Methods

### *5.2.1 Study areas and animal telemetry*

Adult hedgehogs (>600g) were captured by hand at five rural and four urban sites across England, between 2016 and 2019 (See General Methods section in Chapter 2), and GPS/VHF tags (hereafter termed 'tags') (model: Biotrack PinPoint 240; Biotrack Ltd, Dorset, UK) attached (see methodology in Chapter 4). GPS data were screened for inaccurate GPS fixes, and GPS fixes with Horizontal Dilution of Position (HDOP)>5, location error >10 and the number of satellites ≤ 4 were removed. Implausible hedgehog speeds (i.e., over 1 m/s) were also removed following the methodology in Chapter 4.

### *5.2.2 Movement behaviour analysis*

Movement patterns of hedgehogs were analysed using Hidden Markov Models (HMMs). HMMs are a tool for representing probability distributions over sequences of observations using Bayesian networks (Ghahramani, 2001), and have been used to extract information regarding behavioural states of the observed movement of animals (Franke et al., 2006; van de Kerk et al., 2015; Karelus et al., 2019; Beumer et al., 2020). HMMs comprise two components, an observable time series and an underlying, non-observable, state sequence (Langrock et al., 2012; Patterson et al., 2017; Figure 5.1).

When applied to animal movement, the observable time series consists of the animals' step length (Euclidian distance between two consecutive locations) and turning angle (difference in direction for two consecutive locations), whereas the underlying, non-observable behavioural state sequence represents behaviours such as foraging. HMMs estimate both the parameters (i.e., step length and turning angle) that govern movement in each behavioural state, and the probability of transition from one behavioural state to another (Morales et al., 2004).

Two movement behavioural states were defined: foraging (short step lengths and wide turning angles) and travelling (long step length and small turning angles, Figure 5.2) as these were regarded as important behaviours for the ecology of hedgehogs. Step length and turning angles were modelled using gamma and von Mises distributions, respectively (Ellington and Gehrt, 2019; Beumer et al., 2020).

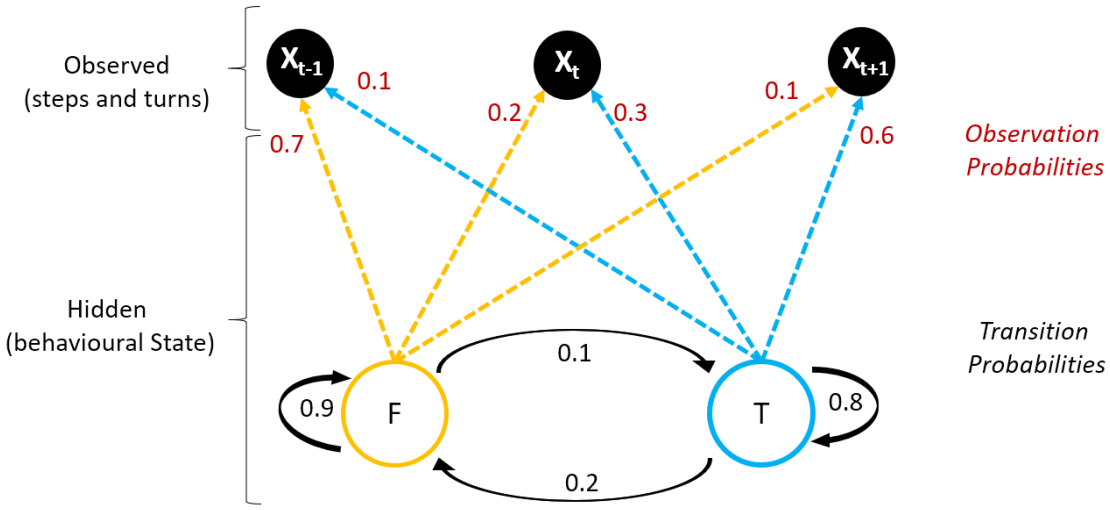



Figure 5. 1. Representation of a Hidden Markov Model comprising two behavioural states: foraging (F; yellow) and travelling (T; blue) for a series of observations X at consecutive times (t). The probability of transition from one state to another is represented in black. The value of the probabilities leaving a specific state must sum 1. Each observation X is also associated with a probability of occurring (observation probabilities; red), which represents the probability of a particular output given a particular state. For example, there is a 70% probability of the individual being in a foraging state at $X_{t-1}$ and only 10% at $X_{t+1}$. The Viterbi algorithm is used to assign the most likely behavioural state to each observation.

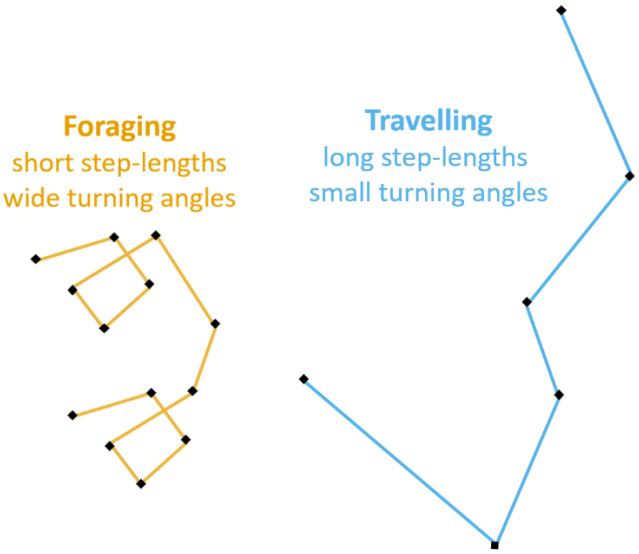



Figure 5. 2. Examples of the patterns of movement displayed by West European hedgehogs (*Erinaceus europaeus*) exhibiting two-movement states. Foraging state was defined by short step lengths and wide turning angles while travelling was defined by long step lengths and small turning angles.

To categorise movements into the two behavioural states, HMMs were first compared from 25 different sets of randomly-chosen starting parameter values to identify the parameters (step length and turning angle) associated with each behavioural state (Michelot and Langrock, 2019). Next, HMMs were undertaken to investigate the effect of five covariates on the transition probabilities between the behavioural states: 1. sex (Dowding et al., 2010), 2. landscape (urban or rural; Riber, 2006; Haigh, O'Riordan and Butler, 2013; Rautio, Valtonen and Kunnasranta, 2013; Rasmussen et al., 2019), 3. distance to gardens (m) (Pettett et al., 2017b), 4. distance to buildings (m) (Pettett et al., 2017b), and 5. distance to roads (Rondinini and Doncaster, 2002), as these variables have previously been shown to influence hedgehog movement. Twenty-nine models (including all possible covariate combinations) were produced, and the most parsimonious model was selected using Akaike's Information Criterion (AIC) (Burnham and Anderson, 2004). The most likely sequence of hidden states to have generated the observation under the best-fitting model was then extracted using the Viterbi algorithm (Zucchini, Macdonald and Langrock, 2016).

To evaluate how transition probabilities are affected by distance to different features of the landscape, i.e., distance to buildings and gardens, the stationary state probability

was explored for different values of the numerical variables (i.e., all distances; Michelot, Langrock and Patterson, 2016; Leos-Barajas and Michelot, 2018). Analyses were undertaken using the *momentuHMM* package (McClintock and Michelot, 2018) in R (version 3.6.1; R Development Core Team, 2019). Distances were were positively skewed, therefore, they werestandardised using z-scores (Norman and Streiner, 2014) prior to analysis, using the function *scale* in R.

### *5.2.3 Habitat selection analysis*

Resource selection analysis (RSA) is the most common ecological tool used to investigate habitat selection of animals, by linking environmental information to location data (Manly, McDonald and Thomas, 1993; Boyce and McDonald, 1999). However, the spatial domain available to the animal remains a concern in the use of RSA, as it assumes that all areas of an animal's estimated home range are equally accessible and that their availability is fixed over time (Matthiopoulos, 2003; Forester, Im and Rathouz, 2009; Northrup et al., 2013). Therefore, step-selection analysis (SSA) has been developed to take into account that not all areas of the availability domain (home range) are equally accessible in space, and that their availability changes over time (Fortin et al., 2005; Thurfjell, Ciuti and Boyce, 2014). Furthermore, SSA deals with concerns regarding serial autocorrelation of animal locations present in GPS data, as points close in time are also expected to be close in space (Arthur et al., 1996; Fortin et al., 2005; Rhodes et al., 2005). SSA resamples step lengths and turning angles to generate random movements, conditional on the previous location (Figure 5.2), by pairing each observed step (i.e., straight lines connecting consecutive locations) with a set of available steps, randomly sampled from the empirical distribution of observed steps or their characteristics (Fortin et al., 2005; Thurfjell, Ciuti and Boyce, 2014).

SSA considers habitat-selection and movement as sequential, rather than simultaneous, processes: habitat-selection is conditional on movement, but movement is assumed to be independent of habitat selection (Avgar et al., 2016). However, these two processes are linked: habitat selection and availability of resources affect animal movement patterns (Avgar et al., 2013). Thus, an extension of SSA, termed 'integrated step selection analysis' (hereafter iSSA), has been implemented to incorporate movement and selection in the same model, taking into account that movement and selection are

linked, both in relation to the landscape and their relationship to one another (Avgar et al., 2016).

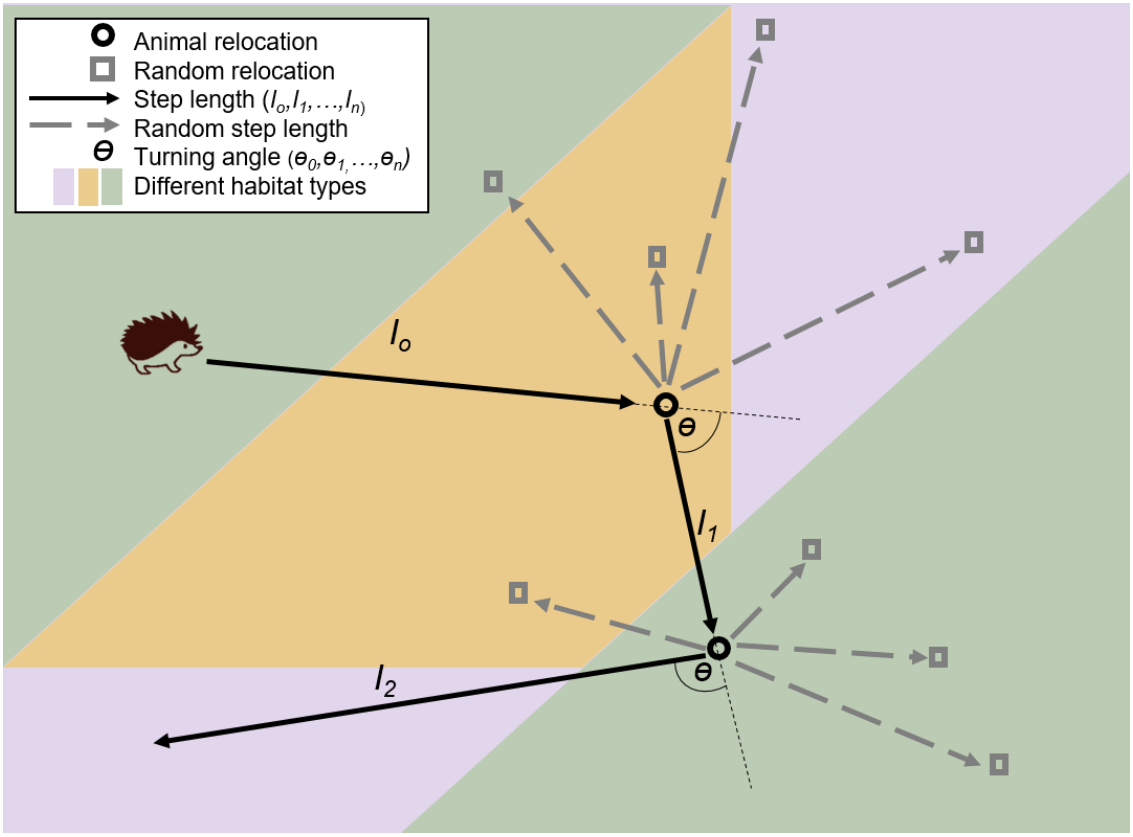



Figure 5. 3. A simplified example of an animal movement pattern into linear step lengths and turning angles. In this example, four random steps (dashed grey lines) have been paired with observed steps (continuous black lines). The endpoint of each step (random and observed) is assigned to a habitat type to investigate habitat selection by comparing used versus available habitats (Figure adapted from Thurfjell, Ciuti and Boyce, 2014).

Habitat selection of hedgehogs in relation to their behavioural state was studied using iSSA (Avgar et al., 2016), and analyses were performed with functions available in the R package *amt* (Signer, Fieberg and Avgar, 2019). To incorporate behaviour in the habitat selection analysis, parameters for foraging and travelling (i.e., step length and turning angle) were used to generate the random steps (Karelus et al., 2019). For example, if the Viterbi algorithm assigned a step as foraging, step length and turning angle were randomly selected from the respective foraging distributions to generate an unused (available) step. With this approach, random steps were generated using step lengths and turning angles associated with the foraging movement pattern. Ten random, unused

(available) points (default number in the *amt* package) were generated for each observed step.

Based on the behavioural patterns extracted from the movement data, habitat selection was investigated in urban and rural landscapes by male and female hedgehogs. Habitat covariates were extracted using OS Mastermap Topography Layers and high resolution (25 cm) Vertical Aerial Imagery (EDINA Digimap Ordnance Survey Service, 2017). Habitat variables were grouped into six categories: amenity grassland (i.e., recreational parks, sports fields, school grounds, allotments, road verges), gardens (i.e., front and back gardens were all treated equally), roads, woodland, pasture and arable land. Spatial queries were performed in ArcGIS 10.3.1 (ESRI, 2015). To account for individual variations in habitat selection, a generalised linear mixed-effect model (GLMM) was fitted with a Poisson distribution. In addition, individual-specific random slopes were included for all covariates except step length (Muff, Signer and Fieberg, 2020). GLMMs were fitted using the Template Model Builder (TMB) via the *glmmTMB* R package (version 0.2.3, Magnusson et al., 2017). Movement pattern maps were generated with the R package *ggmap* (Kahle and Wickham, 2013). All spatial queries were performed in ArcGIS 10.3.1 (ESRI, 2015). All results are given as mean ± SD unless stated otherwise.

## 5.3 Results

Fifty-two individual hedgehogs were tracked across 11 sites, comprising 29 (13 males and 16 females) in urban and 23 (14 females and 9 males) in rural landscapes. Tags remained on individuals between 5- 15 nights (10 ± 2), giving a total of 24 941 location GPS fixes to conduct analyses.

The largest recorded distance travelled on a single night was 4.5 km, by a rural male in Brackenhurst (01/05/2018). A significant difference between the distance (m) travelled per night was found between males (1362 ± 662 m) and females (994 ± 419 m; Mann-Whitney U test: $U(N_{males}=224, N_{females}=224)= 16375$ ; $p<0.05$); and between urban (970 ± 501 m) and rural hedgehogs (1397 ± 585 m; Mann-Whitney U test: $U(N_{urban}=230, N_{rural}=218)= 37389$ ; $p<0.05$), with males travelling further than females and individuals in rural areas travelling further than those in urban areas. In addition, the average movement speeds (m/s) were significantly higher in males (0.065 ± 0.025) than females (0.046 ± 0.015; Mann-Whitney U test: $U(N_{males}=224, N_{females}=224)= 11279$ ; $p<0.05$), and significantly higher in rural (0.0577 ±0.0218) than urban (0.0531 ± 0.0239) individuals (Mann-Whitney U test: $U(N_{urban}=230, N_{rural}=218)= 29662$ ; $p<0.05$) (Table 5.1). No significant correlation was found between the initial weight (g) of the individuals and the mean distance travelled per night ($r_{s\ (50)} =0.26$, $p >0.05$).

### *5.3.1 Movement behaviour analysis*

The model parameters used to fit the HMMs were step lengths of 10.86 ± 7.26 metres and turning angles of 3 ± 0.23 radians for foraging behaviour, and 31.30 ± 20.67 metres and 0 ± 0.77 radians for travelling. Figure 5.4 shows the distributions of step length and angle for all individuals.

Overall, hedgehogs spent more time foraging (68% of observations) than travelling (32%). Hedgehogs in urban areas dedicated 70% and 30% of their activites to forage and travel, respectively, while in rural areas they spent 66% and 34 % of their time foraging and travelling, respectively. However, the percentage of time spent performing each behaviour varied not only by landscape but also by sex. In the urban landscape, females spent more time foraging (91% of female observations compared to 57% for males) and less time travelling (9% for females and 43% for males). In the rural landscape, the percentage of time spent travelling was higher overall, but females still spent more time

foraging (79% of female observations compared to 48% for males) and less time travelling (21% for females and 52% for males).

The HMM that contained the covariates sex, landscape, distance to gardens, and distance to buildings, was the best predictor of the probability of transition between behavioural states (Table 5.2, Appendix F). The model revealed that females were significantly less likely to transition from foraging to travelling than males (β = -0.697; 95% CI = -0.898, -0.496), but significantly more likely to transition from travelling to foraging (β = 0.679; 95%CI = 0.454, 0.904; Table 5.3). Hedgehogs in urban areas were also less likely to transition from foraging to travelling than those in a rural landscape (β = -0.546; 95% CI = -0.782, -0.309; Table 5.3). Further, the increased distance to buildings significantly reduced the probability of transitioning from foraging to travelling (β = -0.127; 95%CI = - 0.226, -0.028), whereas the probability of transitioning from travelling to foraging decreased significantly with increasing distance to gardens (β = -0.229; 95%CI = -0.379, -0.079; Table 5.3).

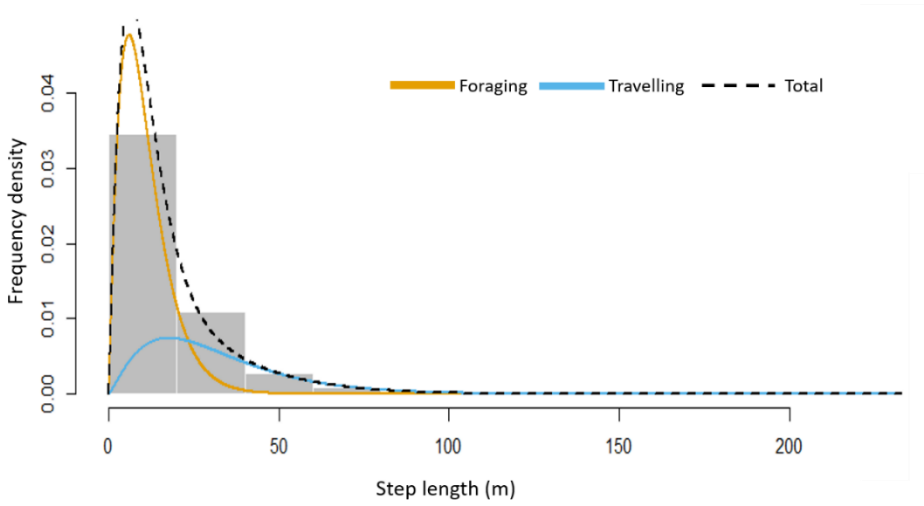
Across both landscapes, there was a sex-effect on the probabilities of foraging or travelling (i.e., differences in the intercepts between males and females) in relation to gardens and buildings: females were more likely to forage than travel, while males showed similar probabilities for both behaviours, although some confidence intervals were large (Figures 5.5 & 5.6). However, no sex-effect was evident on the probability of those behaviours changing with increasing distance (i.e., males and females show similar slopes): the effect of distance to buildings was not evident when foraging or travelling, while the probability of foraging decreased with increased distance to gardens, although confidence intervals were again large (Figures 5.5 & 5.6).

The second-best model to predict transition between the behavioural states also included distance to roads (Table 5.2). However, the effect of increased distance to roads had no significant effect on the probability of switching from travelling to foraging (β = -0.059, 95%CI = -0.215, 0.033), or from foraging to travelling (β = -0.059; 95%CI = -0.164, 0.047).

Table 5. 1. Movement metrics of the West European hedgehogs (*Erinaceus europaeus*) in urban and rural landscapes of England. Results are grouped by landscape type and sex, and include the number of individuals and GPS fixes used in the calculation of the metrics, nightly distances, and speeds recorded. SD=standard deviation, min= minimum, max= maximum.

| Landscape | Sex | Number of individuals | Number of Nights (Number of GPS fixes) | Nightly distance moved (m)<br>Mean (SD) [min-max] | Speed (m/s)<br>Mean (SD) [min-max] |
|---|---|---|---|---|---|
| Urban | Male | 16 | 136 (3143) | 656 (465) [53-3090] | 0.07 (0.03) [0-0.784] |
| | Female | 13 | 94 (1928) | 404 (229) [97-1777] | 0.049 (0.023) [0-0.434] |
| Rural | Male | 9 | 88 (4255) | 1249 (660) [120-3931] | 0.073 (0.025) [0-0.67] |
| | Female | 14 | 130 (6145) | 840 (363) [132-1808] | 0.054 (0.014) [0-0.451] |

**(a)**




**(b)**

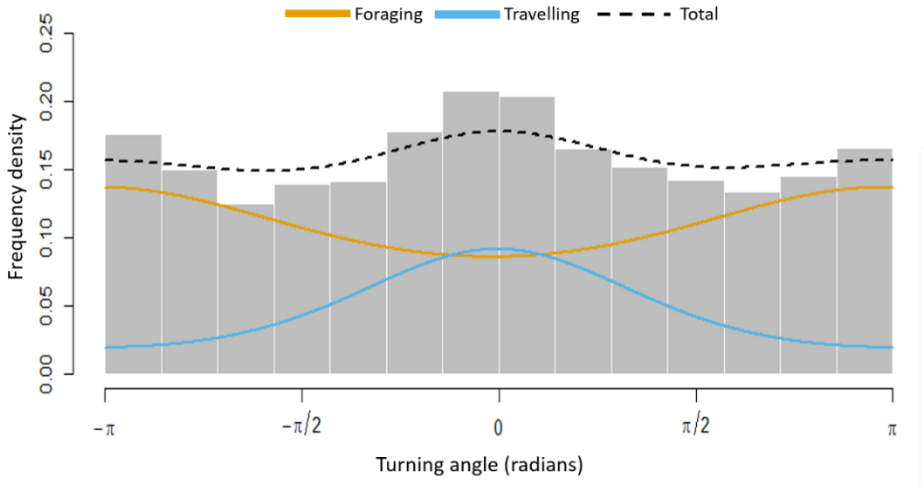



Figure 5. 4. Histograms of movement behaviours (foraging and travelling states) of the West European hedgehog (*Erinaceus europaeus*), showing (a) step length and (b) turning angle between 5-minute relocations, overlaid with state-dependent distributions, as estimated by the HMMs.

Table 5. 2. Top 10 best-fitting Hidden Markov Models (HMMs) describing which covariates best explained the behavioural states (foraging or travelling) and the transition probabilities (switching from one behavioural state to another) of hedgehogs across 9 study sites in England. AIC= Akaike's Information Criterion, $\Delta_i$ = delta AIC, $\omega$= AIC weighting.

| Model | Model | AIC | $\Delta_i$ | $\omega$ |
|---|---|---|---|---|
| M21 | Sex + Habitat + Distance to buildings + Distance to gardens | 199499.7 | 0 | 0.602 |
| M29 | Sex + Habitat + Distance to buildings + Distance to gardens + Distance to roads | 199501.6 | 2 | 0.227 |
| M26 | Sex + Habitat + Distance to gardens | 199502.4 | 3 | 0.153 |
| M25 | Sex + Habitat + Distance to buildings | 199507.3 | 8 | 0.014 |
| M22 | Sex + Habitat + Distance to buildings + Distance to roads | 199509.4 | 10 | 0.005 |
| M23 | Sex + Distance to gardens + Distance to buildings | 199517.2 | 18 | 0 |
| M13 | Sex + Distance to gardens | 199519.7 | 20 | 0 |
| M14 | Sex + Habitat | 199521.5 | 22 | 0 |
| M27 | Sex + Habitat + Distance to roads | 199522.4 | 23 | 0 |
| M24 | Sex + Distance to gardens + Distance to roads | 199523.5 | 24 | 0 |

Table 5. 3. Regression coefficients from the best-fitting model for the probability of transition between the two behavioural states (foraging or travelling) in hedgehogs, where '→' indicates the transition between states. Positive beta values indicate that the transition probability increases with the corresponding covariate while negative beta values indicate the opposite. The reference category (intercept) relates to males and rural landscapes. Confidence intervals that do not encompass zero indicate statistical importance and are marked with asterisks (*).

| Covariates | Foraging --> Travelling | | | Travelling --> Foraging | | |
|---|---|---|---|---|---|---|
| parameter | beta | 95% Confidence Interval | | beta | 95% Confidence Interval | |
| | | lower | upper | | lower | upper |
| Intercept | -1.858* | -2.030 | -1.686 | -2.046* | -2.245 | -1.846 |
| Sex $_{Female}$ | -0.697* | -0.898 | -0.496 | 0.679* | 0.454 | 0.904 |
| Landscape $_{Urban}$ | -0.546* | -0.782 | -0.309 | -0.262 | -0.540 | 0.016 |
| Distance to buildings | -0.127* | -0.226 | -0.028 | -0.096 | -0.231 | 0.039 |
| Distance to gardens | -0.031 | -0.157 | 0.096 | -0.229* | -0.379 | -0.079 |

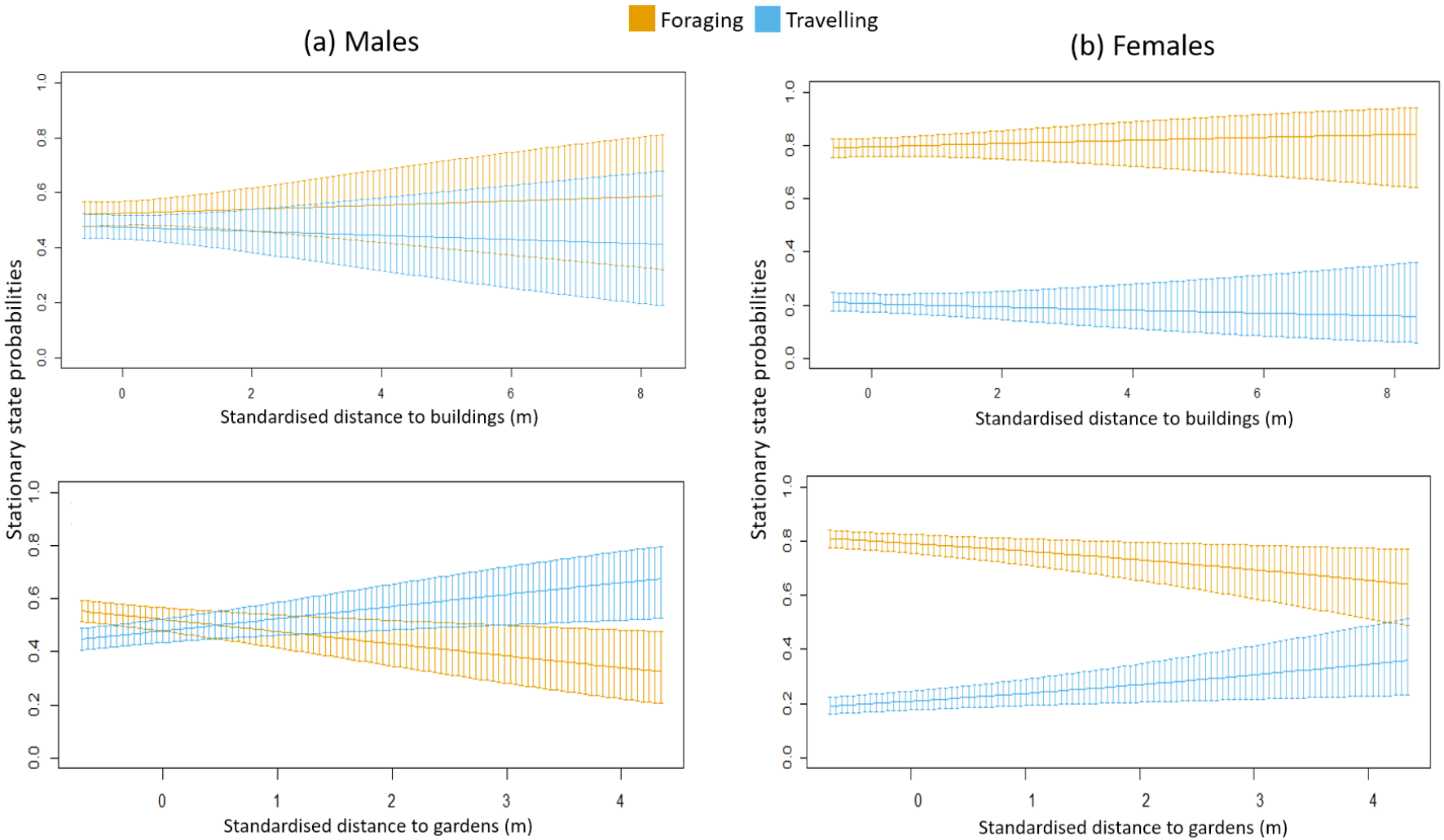



Figure 5. 5. Stationary state probability in urban landscapes for (a) females and (b) males, as a function of the standardised distance to buildings and gardens, with 95% confidence intervals. Numeric variables were standardised using z-scores.

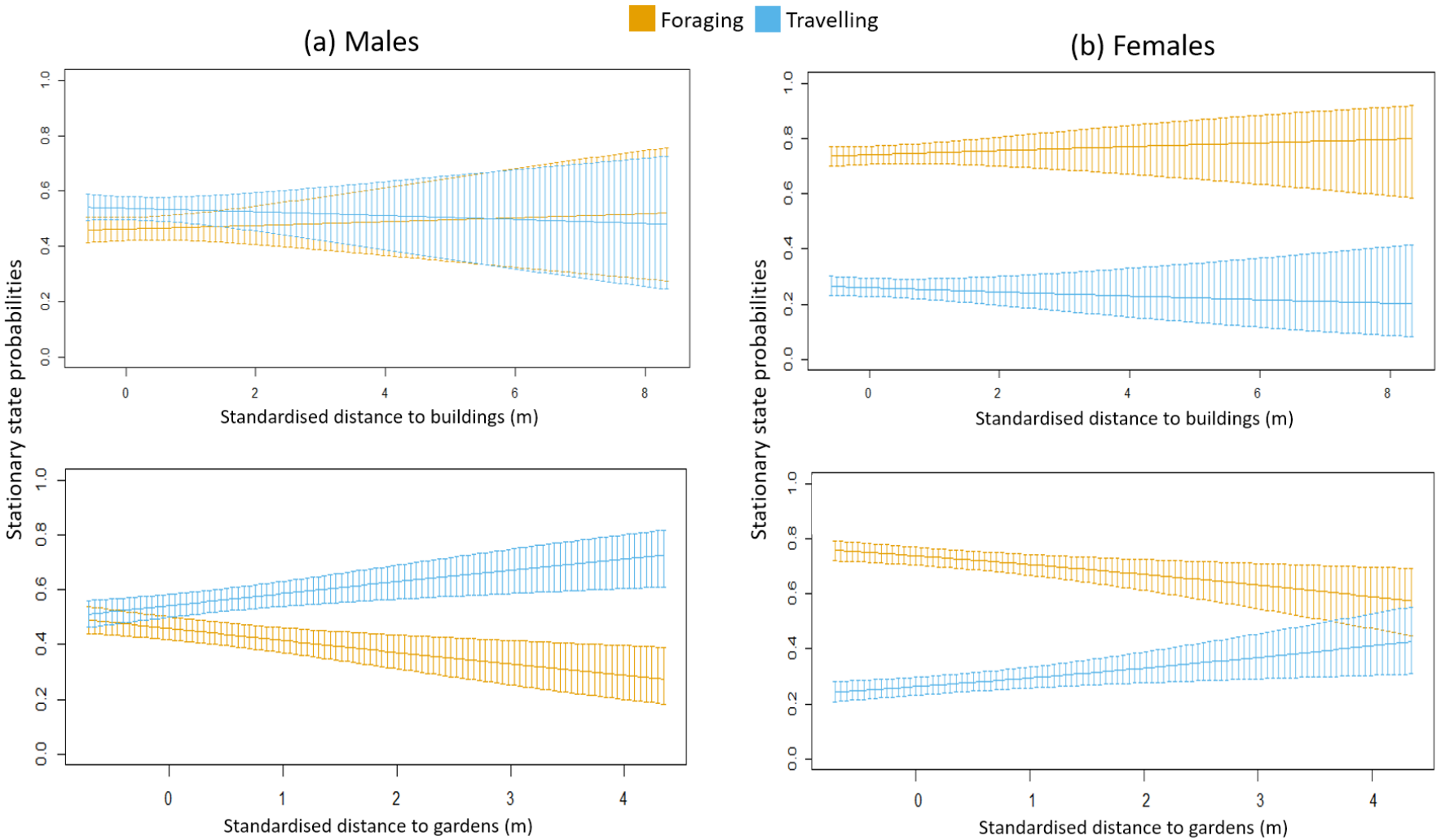



Figure 5. 6. Stationary state probability in rural landscapes for (a) females and (b) males, as a function of the standardised distance to buildings and gardens, with 95% confidence intervals. Numeric variables were standardised using z-scores.


Figure 5.7 (a). Example of the movement pattern of a rural female West European hedgehog (*Erinaceus europaeus*). Yellow lines represent patterns associated with foraging behaviour, and blue lines with travelling behaviour.


Figure 5.7 (b). Example of the movement pattern of a rural male West European hedgehog (*Erinaceus europaeus*). Yellow lines represent patterns associated with foraging behaviour, and blue lines with travelling behaviour.


Figure 5.7 (c). Example of the movement pattern of an urban female West European hedgehog (*Erinaceus europaeus*). Yellow lines represent patterns associated with foraging behaviour, and blue lines with travelling behaviour.


Figure 5.7 (d). Example of the movement pattern of an urban male West European hedgehog (*Erinaceus europaeus*). Yellow lines represent patterns associated with foraging behaviour, and blue lines with travelling behaviour.

### *5.3.2 Habitat selection analysis*

Hedgehogs selected different habitats depending on whether they were travelling or foraging. Habitats were also selected depending on the type of landscape and sex of individuals (Table 5.4).

When foraging (Table 5.4), urban hedgehogs selected gardens and pasture more often than would be expected by their availability, and avoided roads. In rural landscapes, hedgehogs selected gardens, amenity, pasture and woodland (in that order) significantly more than would be expected. Males and females avoided roads and selected gardens, amenity and pasture (in that order), woodland was also selected significantly by females.

When travelling (Table 5.5), urban hedgehogs selected gardens significantly more than would be expected by their availability, and avoided woodland. However, rural hedgehogs showed a significant preference for gardens, amenity, pasture and woodland, in that order. Females selected road, amenity then gardens, and avoided arable, while males selected gardens, amenity then pasture. Arable was not selected in any landscape, neither when foraging nor travelling. In addition, some models did not converge when including the arable variable, due to a lack of GPS fixes recorded at this habitat type and the lack of information to estimate the parameters reliably (Magnusson et al., 2017).

Table 5. 4. Habitat selection of hedgehogs when foraging across urban and rural landscapes, for males and females, showing the estimated coefficients for the habitat variables included in the generalised linear mixed-effect models. Higher coefficients indicate stronger selection in relation to other habitat types within their subgroup. Arable habitat is not included when foraging in the urban landscape, as the model did not converge when including that variable. Habitats showing significant effects are shown in bold. * p< 0.05, ** p< 0.01, *** p< 0.001

| Movement behaviour | Covariates | Habitat | Coefficient | Standard Error | z-value | p-value | |
|---|---|---|---|---|---|---|---|
| Foraging | Urban | Amenity | 0.17399 | 0.0932 | 1.87 | 0.062 | |
| | | Garden | 0.32496 | 0.0294 | 11.05 | **<0.001** | *** |
| | | Pasture | 0.21361 | 0.0957 | 2.23 | **0.026** | * |
| | | Road | -0.61291 | 0.0876 | -7.00 | **<0.001** | *** |
| | | Woodland | -0.80951 | 0.5443 | -1.49 | 0.137 | |
| | Rural | Amenity | 0.24387 | 0.0325 | 7.50 | **<0.001** | *** |
| | | Arable | 0.11738 | 0.0843 | 1.39 | 0.164 | |
| | | Garden | 0.35073 | 0.0458 | 7.66 | **<0.001** | *** |
| | | Pasture | 0.21193 | 0.0354 | 5.99 | **<0.001** | *** |
| | | Road | -0.08623 | 0.0835 | -1.03 | 0.302 | |
| | | Woodland | 0.16675 | 0.0485 | 3.44 | **0.001** | *** |
| | Female | Amenity | 0.2580 | 0.0308 | 8.39 | **<0.001** | *** |
| | | Arable | 0.1423 | 0.0899 | 1.58 | 0.113 | |
| | | Garden | 0.3290 | 0.0301 | 10.92 | **<0.001** | *** |
| | | Pasture | 0.2250 | 0.0361 | 6.24 | **<0.001** | *** |
| | | Road | -0.3451 | 0.1048 | -3.29 | **0.001** | *** |
| | | Woodland | 0.1658 | 0.0497 | 3.33 | **0.001** | *** |
| | Male | Amenity | 0.2323 | 0.0448 | 5.19 | **<0.001** | *** |
| | | Arable | 0.1486 | 0.1365 | 1.09 | 0.276 | |
| | | Garden | 0.3210 | 0.0385 | 8.34 | **<0.001** | *** |
| | | Pasture | 0.2206 | 0.0463 | 4.77 | **<0.001** | *** |
| | | Road | -0.4379 | 0.1300 | -3.37 | **0.001** | *** |
| | | Woodland | 0.0464 | 0.1621 | 0.29 | 0.775 | |

Table 5. 5. Habitat selection of hedgehogs when travelling across urban and rural landscapes, for males and females, showing the estimated coefficients for the habitat variables included in the generalised linear mixed-effect models. Higher coefficients indicate stronger selection in relation to other habitat types within their subgroup. Arable habitat is not included when foraging in the urban landscape, as the model did not converge when including that variable. Habitats showing significant effects are shown in bold. * p< 0.05, ** p< 0.01, *** p< 0.001

| Movement behaviour | Covariates | Habitat | Coefficient | Standard Error | z-value | p-value | |
|---|---|---|---|---|---|---|---|
| Travelling | Urban | Amenity | 0.04591 | 0.0925 | 0.50 | 0.620 | |
| | | Arable | -0.6041 | 0.6542 | -0.92 | 0.356 | |
| | | Garden | 0.29025 | 0.0475 | 6.11 | **<0.001** | *** |
| | | Pasture | 0.3177 | 0.1719 | 1.85 | 0.065 | |
| | | Road | -0.1434 | 0.0908 | -1.58 | 0.114 | |
| | | Woodland | -1.09095 | 0.3047 | -3.58 | **<0.001** | *** |
| | Rural | Amenity | 0.37768 | 0.0485 | 7.79 | **<0.001** | *** |
| | | Arable | -0.41782 | 0.28511 | -1.47 | 0.143 | |
| | | Garden | 0.48677 | 0.0956 | 5.09 | **<0.001** | *** |
| | | Pasture | 0.28161 | 0.0555 | 5.08 | **<0.001** | *** |
| | | Road | 0.17677 | 0.1152 | 1.53 | 0.125 | |
| | | Woodland | 0.1382 | 0.0686 | 2.02 | **0.044** | * |
| | Female | Amenity | 0.3002 | 0.0682 | 4.40 | **<0.001** | *** |
| | | Arable | -1.2528 | 0.5962 | -2.10 | **0.036** | * |
| | | Garden | 0.2803 | 0.1197 | 2.34 | **0.019** | * |
| | | Pasture | 0.1874 | 0.1032 | 1.82 | 0.069 | |
| | | Road | 0.3381 | 0.1123 | 3.01 | **0.003** | ** |
| | | Woodland | -0.0009 | 0.2433 | 0.00 | 0.997 | |
| | Male | Amenity | 0.2601 | 0.0644 | 4.04 | **<0.001** | *** |
| | | Arable | 0.0247 | 0.1547 | 0.16 | 0.873 | |
| | | Garden | 0.3586 | 0.0419 | 8.57 | **<0.001** | *** |
| | | Pasture | 0.2481 | 0.0470 | 5.28 | **<0.001** | *** |
| | | Road | -0.0974 | 0.0824 | -1.18 | 0.237 | |
| | | Woodland | -0.1475 | 0.1512 | -0.98 | 0.329 | |

## 5.4 Discussion

This is the first study extracting hedgehog behavioural states from GPS data, to investigate movement behaviours and their influence on habitat selection across males and females in urban and rural landscapes. Although the study of animal movement behaviour and habitat selection are not new (Morales et al., 2004; Fortin et al., 2005; Patterson et al., 2009; Latham et al., 2011; Patterson et al., 2017; Prokopenko, Boyce and Avgar, 2017), few studies have incorporated movement metrics into habitat selection analyses (but see Karelus et al., 2019). Findings indicate that habitat selection depends on landscape type, with differences found between rural and urban landscapes, and whether hedgehogs are travelling or foraging, where the latter is the most frequent behaviour displayed by hedgehogs. Overall, gardens represent vital foraging grounds and travelling corridors for male and female individuals across urban and rural landscapes. The implications of these findings in the context of hedgehog conservation are discussed, and directions for future research are suggested.

### *5.4.1 Movement behaviour*

This study was able to identify two behavioural states of hedgehogs using GPS telemetry data, and demonstrated that, when active, hedgehogs displayed foraging behaviour most of the time. This study was able to identify two behavioural states of hedgehogs using GPS telemetry data, and demonstrated that, when active, hedgehogs displayed foraging behaviour most of the time. Although different in methodologies, these findings are in accordance with previous studies that found hedgehogs to spend 54% (radio-tracking; Reeve, 1981), 72% (radio-tracking; Berthoud, 1982) and 80% (direct continuous observation; Wroot, 1984) of their active time foraging. I found that the time spent foraging varied not only by sex, as previously shown by Wroot (1984) and Reeve (1994), with females foraging for longer than males, but also by landscape type, as urban hedgehogs spend more time foraging than their rural conspecifics. Males and females typically allocate different times to various behaviours to maximise their reproductive success (Du Toit, 2006). Female mammals tend to invest relatively more time foraging to maximising food intake for the energetically-demanding tasks of producing and rearing offspring, during pregnancy and lactation (Barclay, 1989; Du Toit, 2006). On the other hand, males prioritise gaining or retaining access to reproductive females, diverting time away from foraging (Du Toit, 2006). Indeed, this study shows that males

travel longer nightly distances at higher speeds and have larger home ranges (see Results section in Chapter 4) than females. Further research is needed to evaluate the breeding success of male hedgehogs in relation to the distances travelled, and the trade-offs associated with such energetic and risky activities (e.g., road mortality; Moore et al., 2020).

Urban individuals spent more time foraging than their counterparts in the rural landscape. For example, urban males spent up to 57% of their time foraging compared with 48% for rural males, which are comparable to foraging times obtained by Reeve (1994) and Wroot (1984), as they found rural males spending up to 41% and 58% of their time foraging, respectively. The greater time spent foraging by hedgehogs in the urban landscape can be potentially explained due to the higher availability of food resources found in cities and towns, and less need to travel to find more food (Oro et al., 2013; Cox and Gaston, 2018). Also, rural individuals spent more time travelling than their urban conspecifics, suggesting greater distances between suitable foraging patches in rural landscapes. Indeed, on average per night, rural hedgehogs travelled 1.5x further than urban individuals. The suggestion that food resources may be more abundant and less dispersed in urban areas is further supported by the observation that foraging behaviours were more frequently observed in urban gardens and that individuals were more likely to remain in a foraging state than transitioning to travelling in urban areas. More research is needed to link hedgehog movement to the variation of food resources in both urban and rural habitats, to better understand how the availability and distribution of food impacts foraging behaviour and, ultimately, hedgehog conservation. This study did not quantify habitat quality in terms of food resources, largely due to challenges associated with the heterogeneity of urban areas and access problems, however, incorporating a measure of patch or habitat quality into the movement data would be beneficial for understanding the role of resource quality in influencing movement and ranging behaviour.

The transition between behavioural states was also affected by sex and landscape but had additional influences from the distance to buildings and gardens. Males were more likely to remain travelling, possibly because they mainly focus their activities on finding mates (Morris, 2018), which requires travelling long distances (average: 1.4 km/night). In contrast, females were more likely to remain foraging, to gather food resources to

cope with the high energetic demands of reproduction (Wroot, 1984; Barclay, 1989; Reeve, 1994; Pettett et al., 2017a). In the rural landscape, all hedgehogs had a tendency to be in a travelling state, but there was no clear preference of behavioural state in urban landscapes. This indicates that in the rural landscape, individuals need to spend most of the time travelling, as potentially food resources (Wilson et al., 1999; Macdonald and Feber, 2015) and mates (i.e., lower population density; Schaus et al., 2020) are more dispersed in the landscape. The lack of preference for a behavioural state in the urban landscape supports this argument, as food (Contesse et al., 2004; Prange, Gehrt and Wiggers, 2004; Davies et al., 2009; Davison et al., 2009) and mates (Schaus et al., 2020) are higher in the urban landscape. Hedgehogs were also more likely to be travelling when closer to buildings, probably to avoid disturbances posed by humans (Pettett et al., 2017b; Rast, Barthel and Berger, 2019) or because animals are passing by buildings when travelling between gardens. However, when close to gardens, hedgehogs switched to foraging, indicating that gardens provide vital foraging grounds for hedgehogs (Wroot, 1984).

Although the classification of movement behaviour of hedgehogs in this study can be regarded as simplistic, and individuals are known to display other important behaviours (e.g., mating), only two behavioural states were modelled because they are regarded as essential for the species (Reeve, 1994; Morris, 2018), but also due to the complexity of describing other movement patterns that do not overlap with the two already modelled.

### *5.4.2 Habitat selection*

Although most of the habitat selection studies on hedgehogs have used compositional analyses (e.g., Riber, 2006; Dowding et al., 2010; Haigh, O'Riordan and Butler, 2013; Rodriguez Recio et al., 2013; Pettett et al., 2017b), results here are in line with previous findings, highlighting the importance of gardens for hedgehogs in both rural and urban areas. However, by incorporating movement behaviour into habitat selection, this study provides finer detail of individuals behavioural states in each habitat, increasing our understanding of the importance of different habitat types for the species.

In accordance with previous research (Haigh, O'Riordan and Butler, 2013; Dowding et al., 2010; Braaker et al., 2014; Pettett et al., 2017b), this study found that gardens are strongly selected by urban and rural hedgehogs when foraging and travelling. Gardens not only provide vital resources for foraging, as gardens are full of invertebrates and

other organisms that many species predate (Smith et al., 2006; Jones and Leather, 2012; Prather et al., 2013), but also act as a network of habitats that allow movement across the landscape. Interestingly, although urban hedgehogs are often found on amenity grassland during spotlight surveys (Young et al., 2006; Dowding et al., 2010; Hubert et al., 2011; Pettett et al., 2017a), habitat selection analysis here indicated that hedgehogs do not select amenity grassland, either when foraging or travelling in the urban landscape. These findings are contradictory to previous research that found hedgehog selecting amenity grassland, however, these studies also indicated that the selection was not as strong as for gardens (Rondinini and Doncaster, 2002; Dowding et al., 2010; Braaker et al., 2014). Discrepancies may be due to the different tracking (telemetry vs GPS) and analytical methods employed in the studies. However, what seems to be clear from this and previous research is that gardens are important habitats for the species, with this study providing further details of the resources gardens provide for hedgehogs, both in terms of food and habitat connectivity. Findings of this study highlight the importance of surveying all habitat types when making inferences about habitat usage and selection, and the advantages of GPS devices when studying urban mammals that, due to their elusive ecology and logistics of surveying urban areas, might provide better insight into wildlife behaviour.

In the rural landscape, where gardens are less abundant and more dispersed, individuals must rely on a variety of habitats when foraging, and use more diverse habitats as travel corridors, because they have to move further to access foraging patches. Habitats such as amenity grassland that, in an urban context are not selected, become important habitats for rural hedgehogs (although not as important as gardens). Furthermore, woodland, a habitat that was avoided in urban landscapes, becomes a habitat that is selected in rural landscapes as it can provide resources such as nesting areas (Bearman-Brown et al., 2020). These findings are in line with previous research that found that indeed amenity grassland, woodland and pasture are habitats selected by hedgehogs in the rural landscape (Young, 2005; Riber, 2006; Shanahan, Mathieu and Seddon, 2007; Hof, 2009; Rodriguez Recio et al., 2013).

Interestingly, arable land, which dominates the rural landscape, was not selected in the rural landscape for any behaviour, highlighting that this habitat neither provides resources for foraging, nor functions as a travel corridor for hedgehogs and probably

other species (Donald, Green and Heath, 2001; Robinson and Sutherland, 2002; Mathews et al., 2018). However, previous research indicated that arable land is selected by rural hedgehogs (Young, 2005; Haigh, O'Riordan and Butler, 2013), and management strategies have been suggested to improve this habitat for the conservation of the species (Yarnell and Pettett, 2020). It is important to highlight that when gardens were included in the analysis in previous research, either as 'gardens' (Haigh, O'Riordan and Butler, 2013) or as part of another category (e.g, suburban; Young, 2005), they were prefered over arable land. These findings highlight again the importance of including all habitat types available when making inferences about habitat selection to allow comparison between studies, and the potential discrepancies when using different methodologies.

Roads have been identified as a major contributor to mortality in hedgehogs (Huijser and Bergers, 2000; Moore et al., 2020), but the results show hedgehogs behave differently to the presence of roads depending on the landscape they are in. For example, when travelling and foraging, urban hedgehogs avoided roads in this study, agreeing with previous studies by Rondinini and Doncaster, (2002) and Dowding et al., (2010). However, in rural areas, roads were not avoided by hedgehogs when travelling or foraging, which differs from the findings of Huisjer and Berger, (2000). This could be because roads are not encountered very frequently by rural hedgehogs due to the low density of roads in the rural landscape or because traffic flow at night is lower in rural areas (Havaei-Ahary, 2019) and, therefore, might not impose a significant threat to hedgehogs. Indeed, Wright et al. (2020) found that the probability of hedgehog roadkill was higher in urban habitats, but this may also have been due to urban areas having more hedgehogs (Schaus et al., 2020).

Habitats selected when foraging and travelling differed between males and females. Sex-specific habitat-selection has previously been attributed to differences in breeding strategies (Shanahan, Mathieu and Seddon, 2007; Dowding et al., 2010; Pettett et al., 2017b). Males tend to use a wider range of habitats as they need to cover larger areas to encounter as many females as possible (Dowding et al., 2010; Pettett et al., 2017b). However, selection by females for roads and woodland is unexpected due to the risks of predation and traffic associated with these habitats. This, however, could be due to a confounding effect of landscape type as habitat type was pooled for this part of the

analysis due to sample size. The differences in habitat use between males and females in different landscapes when foraging and travelling (e.g., urban travelling male) was not undertaken due to the small sub-dataset that would have been generated. As previously indicated, hedgehogs use more diverse habitats (e.g., woodland) to obtain resources in rural landscapes. Therefore, the overall selection of roads and woodlands could have been due mainly to rural individuals. Despite this, results of this study provide valuable insight into what behaviours individuals are displaying in different habitats and provides further evidence about the role that the distribution of resources plays in influencing animal movements and habitat selection. Furthermore, the present study adds to the growing evidence of sex-differences in hedgehog movement behaviour and space-use (Dowding et al., 2010; Haigh, O'Riordan and Butler, 2013; Rautio, Valtonen and Kunnasranta, 2013; Rodriguez Recio et al., 2013).

### *5.4.3 Recommendations*

This study did not model the impact of habitat quality on movement and habitat selection of hedgehogs. Food resources found in gardens are expected to differ between different households and characteristics of cities and towns. Also, due to the importance of gardens for hedgehogs across urban and rural landscapes, it is important to obtain a better insight into the resources available in gardens and how these influence the reproductive success and survival of individuals. More research into the quantity and quality of food resources that gardens provide, including supplementary feeding (Hubert et al., 2011; Pettett et al., 2017b), is needed to understand the impact on the behaviour (e.g., increased foraging time) and habitat selection (e.g., nesting sites located near gardens with feeding stations; Gazzard and Baker, 2020) of hedgehogs, potentially identifying mechanisms responsible for hedgehog declines in the urban environment.

Gardens are important habitats for hedgehogs in the rural and urban landscape (Hof and Bright, 2009; Pettett et al., 2017b; Williams et al., 2018a; b), both when foraging and travelling. However, current urbanisation rates are expected to increase the pressure on these habitats, decreasing the proportion of area dedicated to gardens and their availability for wildlife (Baycan-Levent et al., 2002; Mathieu, Freeman and Aryal, 2007; Smith, 2010; Vargas-Hernández, Pallagst and Zdunek-Wielgołaska, 2018).

Hedgehogs strongly select gardens with structures such as bushes, trees, flower/vegetable beds, stones and branches (Braaker et al., 2014). Therefore,

conservation of hedgehogs, which will also benefit other urban mammals due to their role as bioindicator species (Caro, 2010; Goddard, Dougill and Benton, 2013; Johnson, 2017), should focus on promoting the presence of these features in gardens and on creating a well-connected network of gardens by, for example, creating holes in property fences to connect gardens within the urban landscape (e.g. Hedgehog highway; PTES and BHPS, 2020). Such actions will not only increase food resources and nesting sites available for wildlife, but will help to create continuous corridors and act as stepping stone habitats to maintain connectivity and increase movement between habitat patches (Goddard, Dougill and Benton, 2010; McCleery et al., 2012; Braaker et al., 2014).

## 5.5 Conclusions

Animal movement patterns, related to specific behaviours, were taken into account to investigate habitat selection of hedgehogs when foraging and travelling across urban and rural landscapes in England. This study found that hedgehogs select different habitats in the urban and rural landscape, depending on their behavioural state. Hedgehogs select gardens preferentially for foraging and travelling in urban areas. However, in rural areas, where resources are possibly limited and scarce (Hubert et al., 2011), individuals forage over a wider range of habitats and travel more frequently across these different habitats. This study confirms the value of gardens to hedgehogs, as implied in previous chapters of this thesis and in previous work (Dowding et al., 2010; Haigh, O'Riordan and Butler, 2013; Pettett et al., 2017a). Due to the importance of gardens to wildlife, not only for individuals (i.e., provide food, shelter and nesting site) but for the whole population (i.e., promoting movement and habitat connectivity), institutions interested in protecting urban wildlife should focus their activities on ensuring both adequate management of gardens and creating a well-connected network of gardens to promote habitat connectivity and quality.

# CHAPTER SIX

## General discussion and conclusions

Urbanisation produces drastic changes in the environment, with habitat destruction and fragmentation being the most rapid observable consequences (Gaston, 2010; Douglas and James, 2014; James, 2018). Due to the pace that urbanisation takes place, many species are unable to adapt to these changes; however, some species not only survive but thrive in cities and towns (Chace and Walsh, 2006; Bateman and Fleming, 2012). Hedgehogs are a common species across Europe (Wilson and Reeder, 2005), but concerns about their decline have been reported across some European countries (Huijser and Bergers, 2000; Poel, Dekker and Langevelde, 2015; Reichholf, 2015). In the UK, the population of hedgehogs has declined during the last few decades (Battersby and Partnership Tracking Mammals, 2005; Wembridge, 2011; Roos, Johnston and Noble, 2012). Despite declines being reported both in urban and rural areas (Roos, Johnston and Noble, 2012; PTES and BHPS, 2015), urban populations seem to be larger than rural populations (Chapter3; Schaus et al., 2020). However, due to the lack of studies of urban populations, little is known about how hedgehogs respond to urbanisation and which factors are helping the species to persist in cities and towns. This study attempted to understand what services different features of the urban landscape provide for hedgehogs, identify which habitats are important for their activities and use this information to provide further insight into appropriate management to promote hedgehog populations, in both urban and rural areas. These insights were gained using traditional approaches to marking and tracking hedgehogs, combined with contemporary modelling methods used to describe and provide a better understanding of population densities and movement behaviour of hedgehogs across urban and rural landscapes in England.

This study was the first to compare hedgehog density in urban and rural areas and confirmed previous findings that suggested hedgehog density was higher in urban landscapes compared with rural areas dominated by agricultural production. Indeed, on average, hedgehog densities were 7.5 times higher in urban versus rural landscapes (Chapter 3), suggesting that hedgehog populations are more robust in urban areas than in the wider countryside.

Movement behaviour of hedgehogs also differed between urban and rural individuals, with slower speeds, shorter distances and smaller home ranges per night reported in urban individuals (Chapter 4). These differences suggest that hedgehogs in urban areas require less space to find the resources they require on a nightly basis. Chapter 5 also showed that hedgehogs spent more time foraging in urban areas in comparison with rural areas, suggesting that resource density or quality is higher in urban habitats and also that hedgehogs are urban adapters. These findings combined suggest that cities and towns provide areas rich in resources that enable larger populations of hedgehogs to be sustained, while reducing the space requirements of individuals.

Findings from this study can also benefit research and conservation of other species found in the urban landscape (e.g., provide suitable monitoring techniques, highlight the importance of some habitats within the urban landscape, etc.). Whilst these findings are discussed in depth within their respective chapters, the wider implications of this study for hedgehog conservation in both rural and urban areas are discussed here.

### 6.1 Hedgehogs in an urbanised world

Hedgehogs are regarded as biotic indicator species, which are often used to monitor environmental changes and provide warning signals for the health of the environment (Siddig et al., 2016). Hedgehogs are a generalist species, but they mainly predate invertebrates (Yalden, 1976; Wroot, 1984), which also represent the diet of a wider range of species (Pineda-Munoz and Alroy, 2014). Therefore, reports of hedgehog decline raise concerns about the overall quality of the environment and its impact on a wider range of invertebrate predators. However, findings from this study suggest that hedgehog decline might not be general across their distribution, or at least that the rate of decline might be different in rural and urban landscapes, and that urban landscapes are of great value for hedgehogs, as previously suggested (Doncaster, 1994; Morris, 2006; Hubert et al., 2011; Pettett et al., 2017b).

This study found that hedgehogs have higher densities in urban areas compared with rural landscapes, and their space-use behaviour is influenced by the presence of features associated with urban residential development (i.e., the presence of buildings and gardens). Cities and towns provide highly heterogeneous landscapes where the presence of buildings, parks, open land and gardens offer a complex landscape, rich in

elements (Cadenasso, Pickett and Schwarz, 2014), that can sustain high biodiversity (Band et al., 2005). These complex urban landscapes seem to be providing the resources hedgehogs need and, as a result, hedgehogs are living at higher densities in urban areas (Pettett et al., 2017b; Schaus et al., 2020) at lower energetic costs (e.g., movement). Higher densities and reduced movement in urban areas have been suggested to be due to the high availability of food resources that increases the carrying capacity of cities and towns, and reduces the need for individuals to range large distances to find resources (Fedriani, Fuller and Sauvajot, 2001; Shochat et al., 2006; Bateman and Fleming, 2012; Chapman and Byron, 2018). Although this study did not evaluate food provision or similar measurements of habitat quality, it found that gardens are essential habitats for hedgehogs. Despite that further research is needed on the features of gardens that benefit hedgehogs specifically (see *Conservation of hedgehogs and recommendations for future research*), what is clear from this study is that gardens provide important foraging grounds and travel corridors for hedgehogs, presumably delivering resources and habitat connectivity. Gardens are, therefore, vital habitats for the survival and success of hedgehogs in urban areas, which have also been reported for many other urban species (Harris, 1977; Beebee, 1979; Cresswell and Harris, 1988; Carrier and Beebee, 2003; Osborne et al., 2008), and therefore, urban development must ensure the presence, high quality and good-connectivity of these habitats.

This study also found, in accordance with previous studies (Young et al., 2006; Hubert et al., 2011; Parrott, Etherington and Dendy, 2014), that hedgehogs have relatively low densities in rural landscapes. Current agricultural systems are converting rural areas into more homogeneous habitats, reducing the functions and benefits that heterogeneous landscapes provide for wildlife, such as foraging grounds, nesting sites, movement corridors and, ultimately, biodiversity as a whole (Fahrig et al., 2011). Rural landscapes in the UK are mainly dominated by agricultural fields (Hayhow et al., 2019), but some management practices (e.g., use of pesticides, removal of hedge habitats) are reducing invertebrate availability and suitable habitats further. This, in turn, reduces the carrying capacity of rural landscapes for higher vertebrates (Robinson and Sutherland, 2002; Shah et al., 2003; Ridding et al., 2020; Yarnell and Pettett, 2020). Findings here suggest that the population of rural hedgehogs are centred on villages, as also indicated by roadkill studies by Reichholf and Esser (1981), surrounded by unsuitable habitat,

creating fragmented and isolated populations. The low number of rural individuals, aggravated by the possible isolation due to fragmentation by unsuitable arable lands (Williams et al., 2018a), raises concerns about the resilience of the rural populations in the long-term. To provide suitable resources and habitat connectivity for the rural populations, a different set of conservation measurements, such as diversifying farming types and increasing hedgerow and field margin availability, is needed (Yarnell and Pettett, 2020). Such actions will not only help to maintain the current rural populations but also ensure the persistence of the species in the long-term (Yarnell and Pettett, 2020).

This study has provided further evidence that hedgehogs can respond to landscape modifications, whilst exploiting the resources that cities and towns offer. Findings here suggest that residential areas are associated with high hedgehog density and, therefore, an increase in these may not be necessarily negative for hedgehogs, in fact, may be beneficial for the status of the species, as long as the appropriate features (e.g., well-connected network of gardens) are included in their design. As urban development is expected to increase (United Nations, 2018), instead of solely focusing on the detrimental impact that urbanisation can cause on wildlife worldwide, researchers should also focus on understanding how species respond and adapt to this environment, and identify vital habitats and landscape features that help wildlife to face the challenges imposed by increased anthropogenic development. Such information could be then used to inform urban planning to promote the persistence of wildlife.

## 6.2 Importance of study

This study found that, despite hedgehogs seeming to be in decline across the UK (Battersby and Partnership Tracking Mammals, 2005; Wembridge, 2011; Roos, Johnston and Noble, 2012), population estimates and trends of hedgehogs have been based on very limited data from studies without robust methodology and experimental designs. Therefore, current nationwide estimates are not reliable. Although previous research suggested that densities of hedgehogs were higher in urban areas, this is the first robust comparative study to estimate population densities across three rural and five urban areas in England, providing data currently unknown for the species, and confirm that populations of hedgehogs are higher in urban landscapes (chapter 3).

The non-invasive camera trapping method (i.e., REM) and sampling design implemented in this study (chapter3; Schaus et al., 2020) provide a robust study design, which is able to detect 25% of population changes with high probability on consecutive surveys (e.g., years). The outcome of this study (chapter 3) demonstrates a robust tool for estimating and monitoring populations that does not require invasive capture techniques. This can be beneficial not only for hedgehogs but many other species that are difficult to survey due to their elusive or nocturnal behaviour. Furthermore, the results of Chapter 3 help to meet objective 2 of the current conservation strategy of hedgehogs in the UK (Johnson, 2017), which calls for more research into cost-effective survey methodologies to estimate density, especially with regards to urban areas, where there is a lack of population studies despite the species being more abundant in these areas (Schaus et al., 2020). The study design implemented in chapter 3 could be replicated on a large scale to obtain long-term data, currently unknown, about the status of the population. Once reliable population estimates are obtained, research could focus on identifying drivers of hedgehog decline on large and local scales and assess the efficiency of current conservation actions. Furthermore, an urban stratification approach could be used to identify how different types of urban areas (e.g., inner-city, suburban and fringe areas) and degrees of urbanisation impact the population densities of hedgehogs and help researchers to identify features of cities and towns that are most beneficial for hedgehogs.

The possibility of implementing this method as part of citizen science projects furthers its importance in the field of urban ecology as it provides a means to obtain population data on urban species, which can be challenging due to the logistics of surveying urban landscapes (e.g., access to private land). The method has great potential for use in areas where communities of people could work together to deploy the large number of camera traps needed. Such communities already exist in the UK (e.g., Hedgehog Street; PTES and BHPS, 2020) and could be organised to set up monitoring programs to obtain large-scale, long-term population densities and trends following the framework suggested in chapter 3 (Appendix A). The perception of citizens about wildlife is vital for the management of urban species (Bremner and Park, 2007; Verbrugge, Van Den Born and Lenders, 2013; Novoa et al., 2017), and positive attitudes towards some species can be highly beneficial for the conservation and management of other wildlife (Toomey and

Domroese, 2013). Therefore, involving communities in the monitoring of species will help researchers obtain the much needed, yet challenging to obtain, data of urban species and will also increase wildlife awareness and conservation among communities. This will provide communities with motivation and knowledge that will benefit the persistence of species in cities and towns further (Cooper et al., 2007; Bonney et al., 2009; Dickinson, Zuckerberg and Bonter, 2010; Parsons et al., 2018b).

The outcomes of this research are of great importance for wildlife movement research, as this study has implemented a novel approach to incorporate behaviour into habitat selection using high-frequency GPS movement data and contemporary modelling techniques (chapter 5). This approach provides tools for researchers to identify important habitats for the different ecological needs of animals. This study found that despite an increase in the number of movement studies of hedgehogs (e.g., Glasby and Yarnell, 2013; Rodriguez Recio et al., 2013; Braaker et al., 2014; Rast, Barthel and Berger, 2019), there is a lack of comparative movement studies that help our understanding on the responses of hedgehogs to urbanisation. Therefore, the findings of this study have provided high resolution and fine-scale movement metrics for two major landscape types in the UK, and demonstrated how hedgehog movement and behavioural state is influenced by features of the landscape such as gardens and buildings.

The findings of this research provide evidence that hedgehogs are able to inhabit in cities and towns by exploiting habitats associated with humans (i.e., gardens), reducing the space requirement and consequent energy costs associated with travelling in comparison with rural habitats. Despite urbanisation being known to increase fragmentation and isolation of populations on a large scale (Gaston, 2010; Douglas and James, 2014; James, 2018), at a smaller scale, such fragmentation might not be as detrimental, as individuals can still move and access different areas of the cities on consecutive nights. Furthermore, on some occasions, urban individuals crossed common barriers to movement (e.g., roads), and carried out exploratory trips into areas outside cities (e.g., Figure D-39, Appendix D), indicating that individuals can move through fragmented landscapes even at a larger scale. However, as these movements were not common, investigating the impact for individuals is needed as such movements may be a great risk to the animals and result in death or injury. Further investigation is also needed into the degree of permeability of these landscapes and how much

fragmentation hedgehogs can cope with before populations become completely isolated.

### 6.3 Limitations of work

Although this research was conducted rigorously, and findings here provide a sound basis for further work, there are some limitations that should be mentioned.

Firstly, the urban study areas included in this study were mainly dominated by residential areas (Figure 2.2). Likewise, the rural areas mainly compromised mixed farming landscapes in the proximity of a cluster of buildings (i.e., university campus; Figure 2.3). Inner cities, industrial estates and other urban and rural landscape types are likely to provide contrasting resources for hedgehogs, so investigating hedgehog persistence, density and movement in these areas would provide a more holistic picture of the current state and behaviour of the species. Therefore, wider inference across the rest of the urban and rural landscape should be made with caution, considering the specifics of the landscapes studied here.

Secondly, due to battery restriction, this study collected movement data over a relatively short period of time (10 ± 2 days). Data over longer periods of time would provide more insight into the behaviour of individuals and how they use the landscape in the long term. This information would help researchers to identify other features that might be of importance for the long-term persistence of the species in the urban landscape. With the current technology, this might require reducing the frequency of fixes recorded by the GPS tags, but this can result in fewer details of movement patterns. Nevertheless, such an approach will help to answer research questions on different temporal and spatial scales. What is evident from this study is the great potential of GPS devices to provide insight into behaviours that would otherwise be difficult to observe and record, especially of elusive nocturnal species.

Thirdly, due to the lack of individuals tracked during the pre-hibernation period (i.e., August- September), the effect of seasonality on movement patterns and habitat selection of hedgehogs was not investigated. However, hedgehogs are known to show different movement behaviours depending on the time of the year (Riber, 2006; Dowding et al., 2010; Haigh, O'Riordan and Butler, 2013; Rasmussen et al., 2019; Rautio, Valtonen and Kunnasranta, 2013; Rodriguez Recio et al., 2013), and such seasonal

difference varies between males and females (Rautio, Valtonen and Kunnasranta, 2013): males show greater variation in home range size, and larger home ranges during the mating season; females have larger home ranges during pre-hibernation (Rautio, Valtonen and Kunnasranta, 2013). Therefore, an important interaction between season and sex is found in hedgehogs, which is expected to influence not only their home ranges but further movement metrics (e.g., speed, nightly distance travelled) and habitat selection too. Further research on movement and habitat selection should discern between the time of year, to better identify which habitats are of vital importance for the seasonal needs of the species. Answering such specific questions would require large datasets, which are logistically challenging to obtain, but such an approach could provide a better insight into the habitat requirements of hedgehogs across different behaviours. Despite this study not investigating differences in season, it has provided a sound methodology to study the importance of different habitats for different behaviours throughout the active period.

Finally, it is important to mention that although the study design implemented here aimed to ensure population closure by delimiting the study areas by roads, this assumption was not met, as proven by the large movement of some individuals who left the study area (Appendix D). These, however, do not impact the results of this study as the REM and SCR are quite robust to closure assumption (Chapter 3), and exploratory trips were removed from the home range analysis (Chapter 4).

### 6.4 Conservation of hedgehogs and recommendations for future research

Understanding the drivers behind the differences in population densities and movement behaviour of hedgehogs between urban and rural landscapes will help to identify the factors influencing hedgehog decline, and implement conservation management to stabilise and enhance hedgehog populations in the future. Therefore, the conservation of hedgehogs will benefit from the implementation of monitoring schemes in urban and rural landscapes to obtain reliable population density estimates and provide researchers with robust population trends. These will aid our understanding of the current status of the species on a national scale and identify the possible reasons behind their decline.

Due to the different characteristics of urban and rural landscapes, and how these are impacting hedgehogs, conservation management of the species should aim for different

strategies in different landscapes. In the rural landscape, further research is still needed on the impact of current agricultural schemes on resource availability and habitat connectivity, and how these changes impact populations of hedgehogs, in order to implement specific management actions. Conversely, while conservation of urban hedgehogs should focus efforts on identifying specific features of gardens (see below), it should continue increasing citizens' awareness and participation in wildlife gardening, informing of the vital role that gardens play for wildlife. Although wildlife gardening is a common practice in the UK, the availability of gardens in inner-cities is limited, decreasing the availability of important habitats for wildlife (Gaston et al., 2007). On a larger scale, hedgehog conservation should advocate sustainable urban planning to promote not only the presence of gardens and other green spaces but a well-connected network of these habitats to promote sustaining a healthy population in the long term. Such actions will help the prevalence of the hedgehog and many other urban species (Goddard, Dougill and Benton, 2010).

An exciting avenue for further research could include investigating how the quality and distribution of gardens affect the carrying capacity of cities and hedgehogs' space and habitat use behaviour. We need to improve our knowledge about the elements that make a good garden for nesting, or indicate how good gardens are for food availability and foraging, and which features promote travelling between gardens. Research on how different characteristics of gardens such as size, composition, fencing, and food resources influence their use by hedgehogs is also needed. The number of gardens used by urban hedgehogs was variable, from 1 to 32 gardens on a single night, suggesting that important characteristics influence when gardens are used. Whether such variability remains in the long-term should also be explored. Understanding the minimum number of gardens and the essential features that gardens should have in order to promote the persistence of a healthy population of hedgehogs is vital to better inform garden practices and focus conservation objectives on a smaller scale.

Another area of research relates to the implications of supplementary feeding on urban mammals, as this is increasing in popularity across the globe (Robb et al., 2008; Davies et al., 2009). Higher food availability increases carrying capacity (Chapman and Byron, 2018) and population density (Fedriani, Fuller and Sauvajot, 2001), promoting unnatural proximity of individuals, which can increase pathogen transmission (Murray et al., 2016).

Supplementary feeding can also affect dispersal (Robb et al., 2008). However, as most studies are based on bird species (e.g., Galbraith et al., 2015), our understanding of the impacts that supplementary feeding has on mammals is limited. Interdisciplinary research to investigate how supplementary feeding affects the movement of hedgehogs and the broader health and genetic implications for the population is urgently needed as the presence of hedgehogs is positively associated with anthropogenic food resources (Baker and Harris, 2007; Hubert et al., 2011; Pettett et al., 2017b).

Finally, another avenue for further research could include examining landscape connectivity to identify the degree to which the landscape facilitates or impedes movement between resource patches (small scale) and populations (large scale). Ensuring landscape connectivity is a global conservation concern due to habitat fragmentation worldwide (Beier, Noss and Nosst, 1998; Crooks and Sanjayan, 2006; Aronson et al., 2017). With advances in technology and the utility of GPS devices that allow movement data to be obtained for small mammals on different temporal and spatial scales (Tomkiewicz et al., 2010; Seidel et al., 2018), the energetic cost of movement could be evaluated between and within cities and towns. By studying landscape connectivity, with simple resistance-based models such as least-cost path analysis, researchers could identify areas of the landscape where movement is favoured (Zeller, McGarigal and Whiteley, 2012; Fuller et al., 2015; Braaker et al., 2014). Different cities and towns where hedgehogs are found have different degrees of urbanisation (Schaus et al., 2020) and, therefore, movement responses due to different landscape connectivity are expected to vary (Balbi et al., 2019). Hedgehog research in the UK, where the species is under threat (Battersby and Partnership Tracking Mammals, 2005; Wembridge, 2011; Roos, Johnston and Noble, 2012), will benefit the species by identifying highly functional movement corridors that allow individuals to access the resources they need and promote connectivity among populations despite habitats being fragmented. Furthermore, the role of urban gardens in habitat connectivity needs to be assessed and the features of gardens that promote connectivity identified. For example, the hedgehog highway campaign (PTES and BHPS, 2020), promotes cutting holes in garden fences to increase habitat connectivity and facilitate hedgehog movement in the urban landscape (Hof and Bright, 2009). The impact of these actions

needs to be assessed to identify if landscape connectivity has been increased and hedgehogs are indeed using these holes.

## 6.5 Conclusions

This study has provided previously unknown, insight into the responses of hedgehogs to urbanisation. This is the first study to implement a non-invasive camera-trapping method to study urban population densities of a species whose individuals cannot be distinguished from natural markings. The methodology implemented here could be used by citizens to monitor long-term, large-scale population trends of hedgehogs and many other urban mammals; data that is currently lacking and much needed. Findings here indicate that, like many other urban species, hedgehogs can find suitable habitat in cities and towns where they can persist and reach higher densities than in agricultural landscapes.

This is also the first study to extract movement behaviour from high-frequency GPS data of hedgehogs to explore space-use and animal movement across urban and rural areas, and highlight the vital importance of gardens for different ecological requirements of the species. Conservation of hedgehogs in urban areas should, therefore, focus on better management of urban gardens, while further research should aim to identify specific features within gardens that encourage wildlife.

Despite urbanisation being detrimental for some species as they struggle to adapt to drastic landscape changes, habitat loss and fragmentation, other species are able to exploit the resources that cities and towns offer and survive in these human-made environments. Further studies should explore how various features of the urban landscape are exploited by different species to encourage wildlife-friendly urban planning that promotes the persistence of urban species and the co-existence of humans with nature and wildlife.

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## Appendices

**Appendix A.** Citizen science framework for implementing the Random Encounter Model (REM)

The averaged REM parameters (aveREM) approach described in this article is able to detect a 25% change in hedgehog density in both habitats with >90% power. This approach is also a promising solution to the challenge of large-scale and long-term species monitoring. We suggest implementing the Random Encounter Model (REM) as a contributory model (*sensu* Shirk et al., 2012) in a citizen science monitoring study. We propose a 3-stages framework: pilot study, monitoring study, and study output (Figure A-1).

*1. Pilot study*

To apply this framework at a national scale for a specific species, pilot studies across a range of habitats in different locations (study areas) are needed to obtain the survey-specific parameters. Within each study area, random camera trap (CTs) locations are generated and fieldwork is carried out by researchers to measure the survey-specific parameters (angle, distance and speed) and obtain densities using the survey-specific REM (ssREM) approach. Once measurements of the parameters have been collected from a representative sample of habitats, the averages of each of the parameters across surveys are obtained to calculate densities using the averaged parameters REM (aveREM) approach. The pilot study finishes when enough measurements of the parameters have been obtained so that the densities estimated by the ssREM and aveREM are comparable.

*2. Monitoring study*

The monitoring study requires the participation of a starting pool of citizen scientists in community engagement activities (i.e., recruiting further participants) and camera trapping surveys (i.e., placement and collection of camera traps, and data reporting). At this stage, researchers need to provide camera trap training to all the participants. For the long-term implementation of the project, the same areas will be surveyed along the years. For successive surveys, assuming participants are still engaged with the project, only camera trapping surveys would be needed as the same CTs locations will be re-

used. If any participant decides to discontinue their involvement in the study, a small community engagement activity will be required to find new participants and relocate the camera trap location(s).

*3.Study output*

Study output is the final stage and involves data analysis and dissemination of results to the local and research community. Researchers will receive raw data (i.e., videos) from the citizen scientists and, using the aveREM parameters estimated in the pilot study, estimate the densities.

By including diverse habitat types into the study areas, a national population estimation can be obtained using camera traps and the averaged REM approach. In this study, we have carried out the pilot study needed to survey hedgehogs, so that future studies use the parameters obtained here to estimate densities of hedgehogs at other sites. Therefore, a citizen science project to monitor hedgehogs in the United Kingdom will require only the last two stages. Any other monitoring programs focused on a different species to be included in this framework would require to follow all three stages described

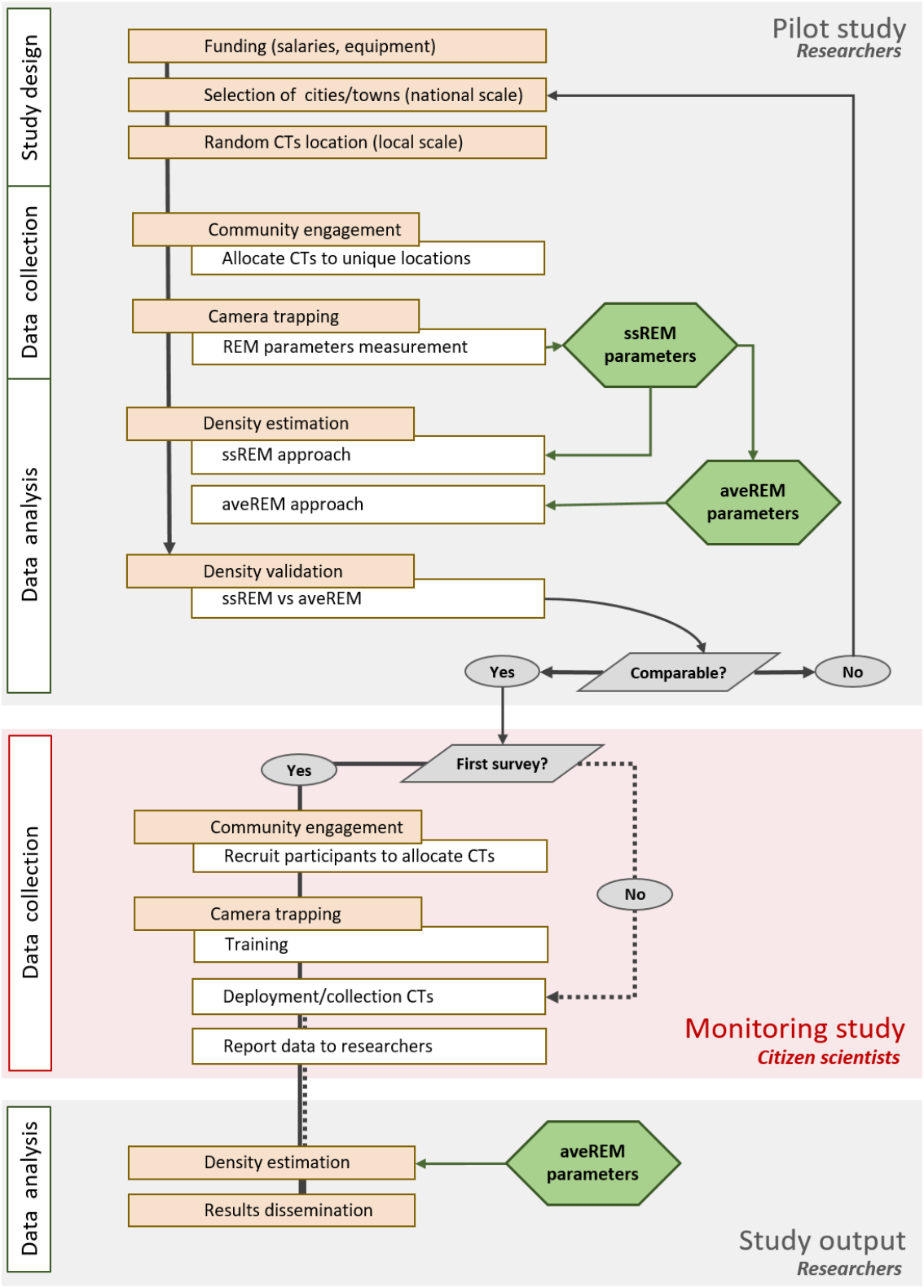



Figure A-1. Citizen science monitoring framework based on the use of the Random Encounter Model. Flowchart to implement the Random Encounter Model (REM) in a contributory model of citizen science monitoring study. We propose a 3-stages framework: pilot study, monitoring study, and study output. CTs =camera traps; ssREEM= survey-specific REM; aveREM= averaged REM.

**Appendix B.** Maps representing the study areas and the GPS fixes recorded by all individuals at each urban (n=5) and rural (n=6) surveys.

(a) Southwell 2016

(b) Ipswich 2017

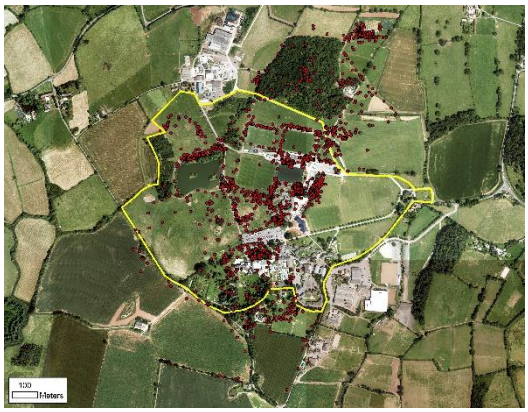
(c) Ipswich 2018

(d) Brighton 2018

(e) Brighton 2019

Figure B-1. Study areas (yellow lines) and GPS fixes (red dots) generated by all hedgehogs in each urban study site between 2016-2019 in England.

(a) Hartpury 2017

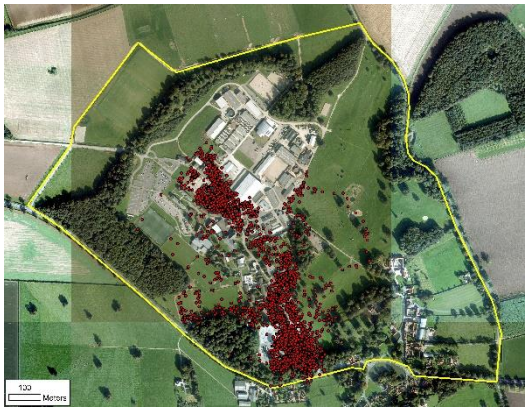


(b) Brackenhurst 2017

(c) Brackenhurst 2018

(d) Sutton Bonington 2018

(e) Bishop Burton 2019



(f) Riseholme 2019

Figure B-2. Study areas (yellow lines) and GPS fixes (red dots) generated by all hedgehogs in each rural study site between 2016-2019 in the England.

**Appendix C.** Maps representing the GPS fixes recorded by each individual at each urban (n=5) and rural (n=6) surveys.

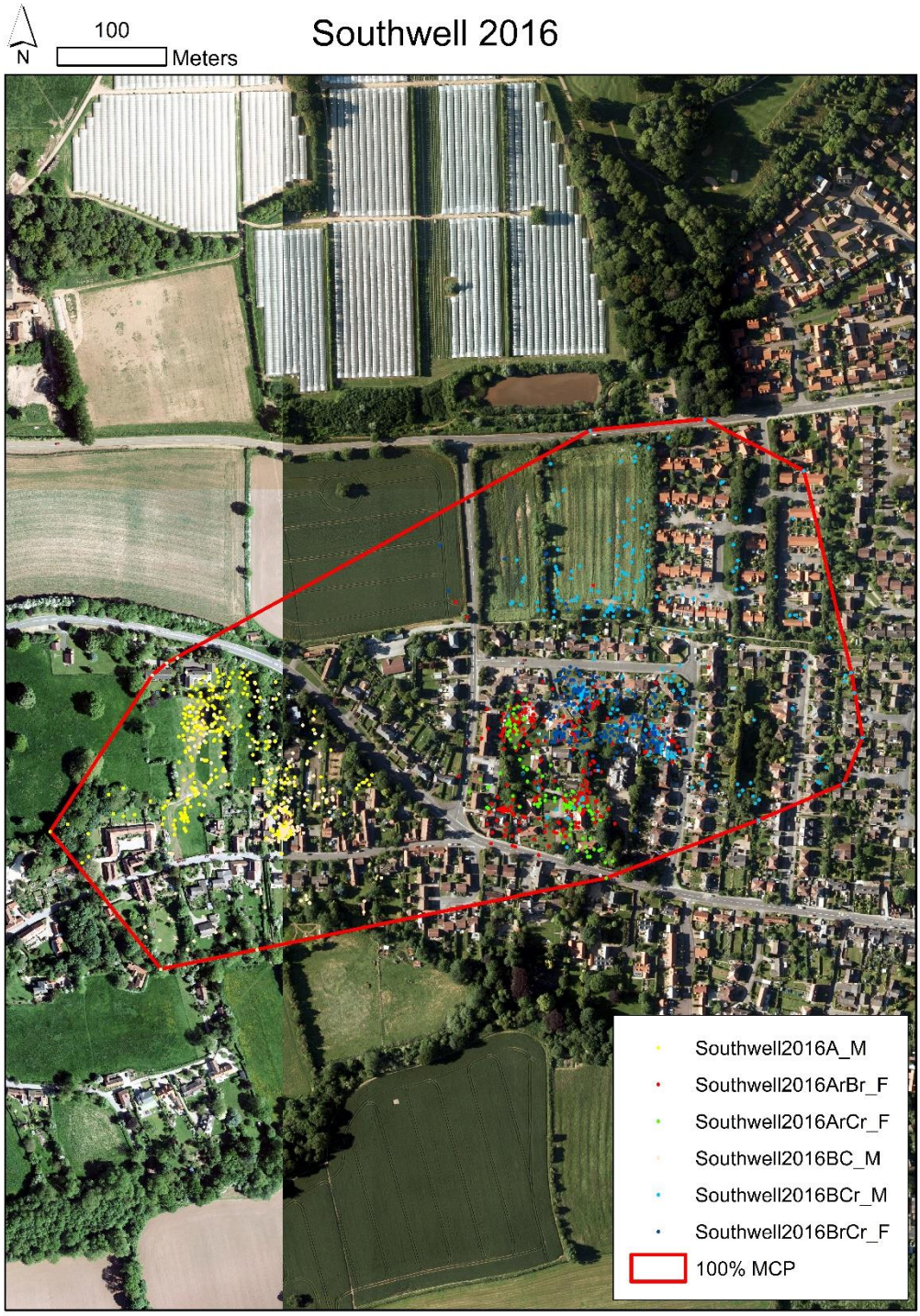



Figure C-1. Movement data of West European hedgehogs (*Erinaceus europaeus*) in Southwell, 2016. Colours represent GPS fixes recorded by different individuals; red line represents the 100% Minimum Convex Polygon encompassing all GPS fixes recorded during the survey period.


Figure C-2. Movement data of West European hedgehogs (*Erinaceus europaeus*) in Ipswich West, 2017. Colours represent GPS fixes recorded by different individuals; red line represents the 100% Minimum Convex Polygon encompassing all GPS fixes recorded during the survey period.


Figure C-3. Movement data of West European hedgehogs (*Erinaceus europaeus*) in Brighton, 2018. Colours represent GPS fixes recorded by different individuals; red line represents the 100% Minimum Convex Polygon encompassing all GPS fixes recorded during the survey period.

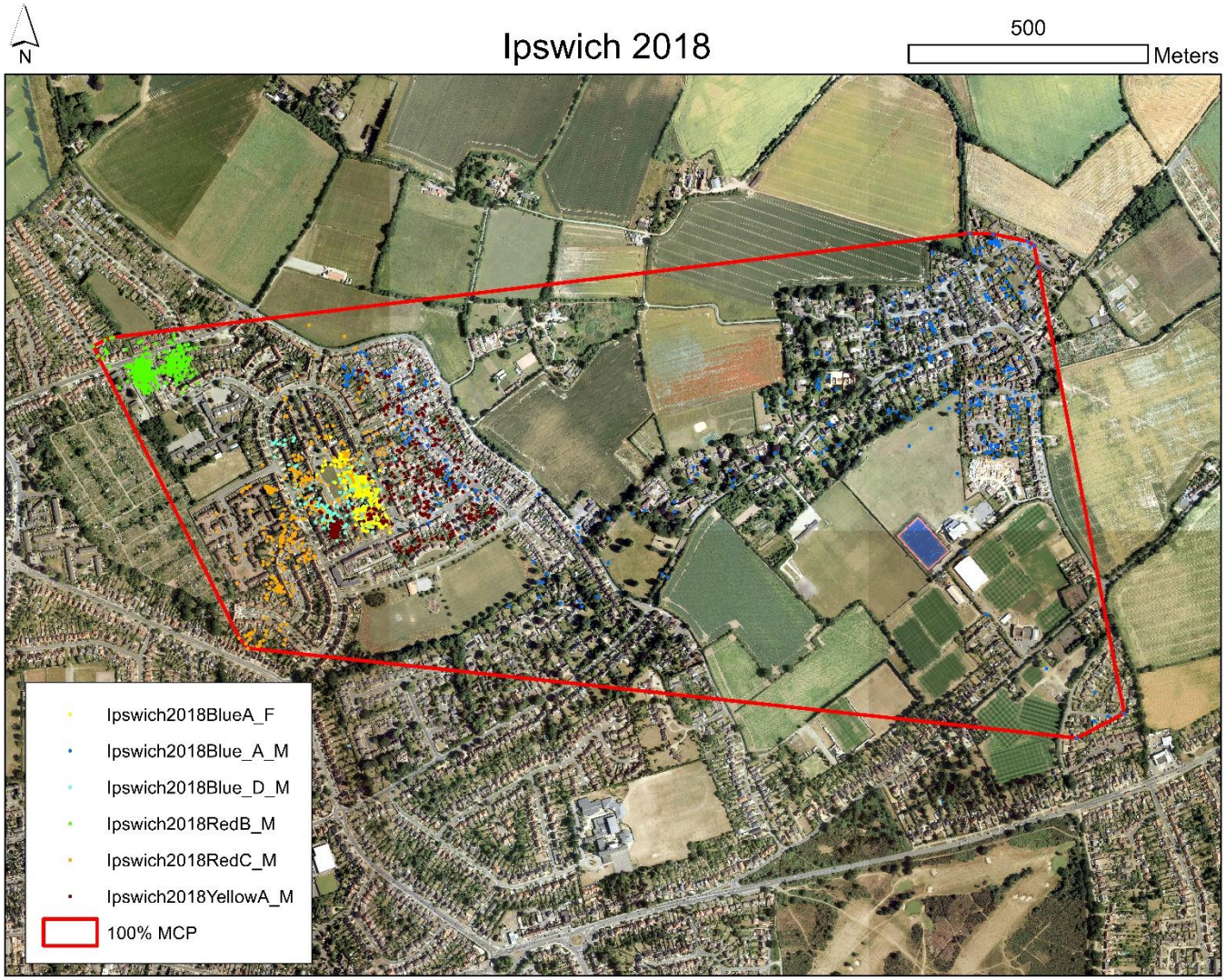



Figure C-4. Movement data of West European hedgehogs (*Erinaceus europaeus*) in Ipswich East, 2018. Colours represent GPS fixes recorded by different individuals; red line represents the 100% Minimum Convex Polygon encompassing all GPS fixes recorded during the survey period.


Figure C-5. Movement data of West European hedgehogs (*Erinaceus europaeus*) in Brighton, 2019. Colours represent GPS fixes recorded by different individuals; red line represents the 100% Minimum Convex Polygon encompassing all GPS fixes recorded during the survey period.

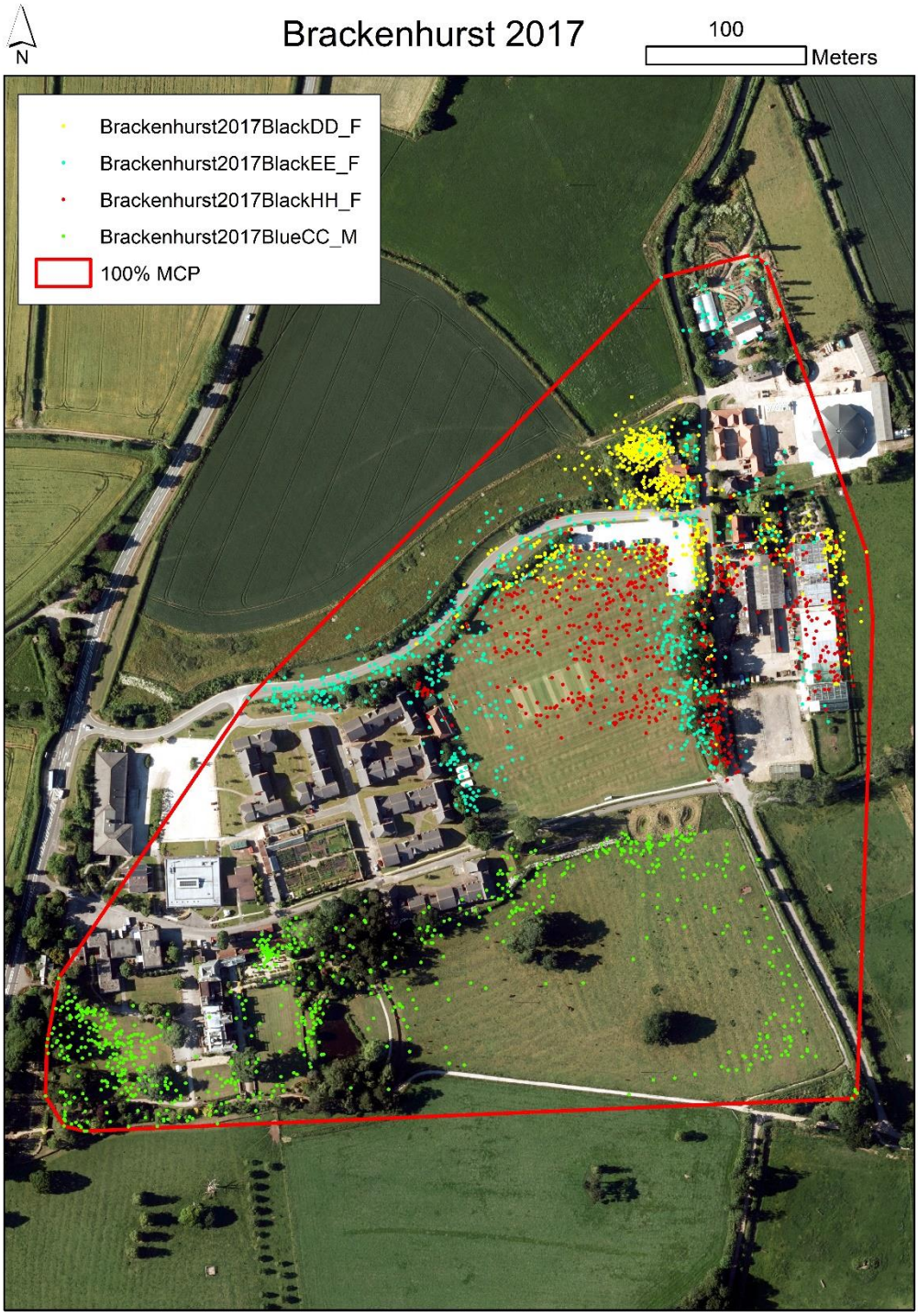



Figure C-6. Movement data of West European hedgehogs (*Erinaceus europaeus*) in Brackenhurst, 2017. Colours represent GPS fixes recorded by different individuals; red line represents the 100% Minimum Convex Polygon encompassing all GPS fixes recorded during the survey period.

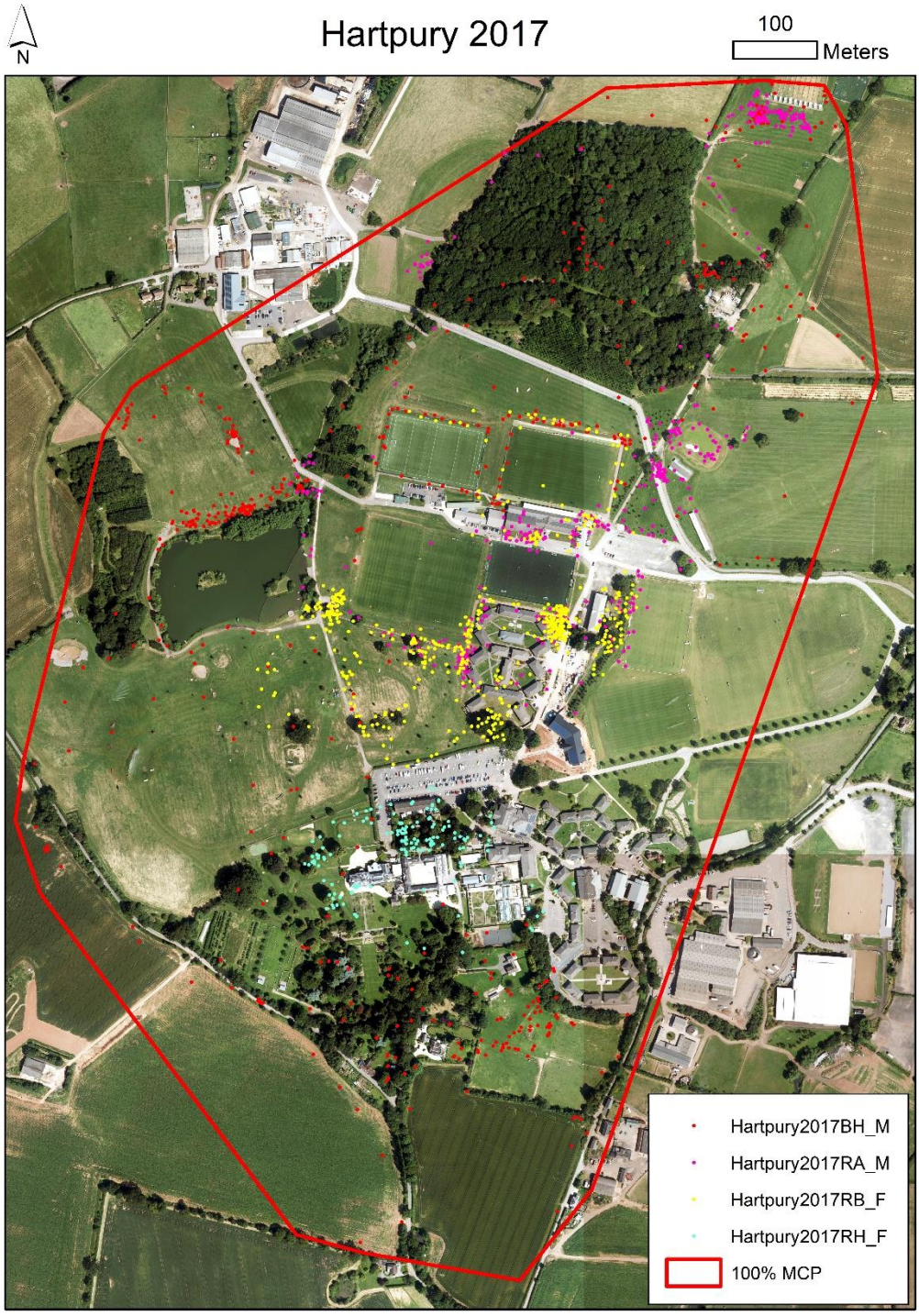



Figure C-7. Movement data of West European hedgehogs (*Erinaceus europaeus*) in Hartpury, 2017. Colours represent GPS fixes recorded by different individuals; red line represents the 100% Minimum Convex Polygon encompassing all GPS fixes recorded during the survey period.

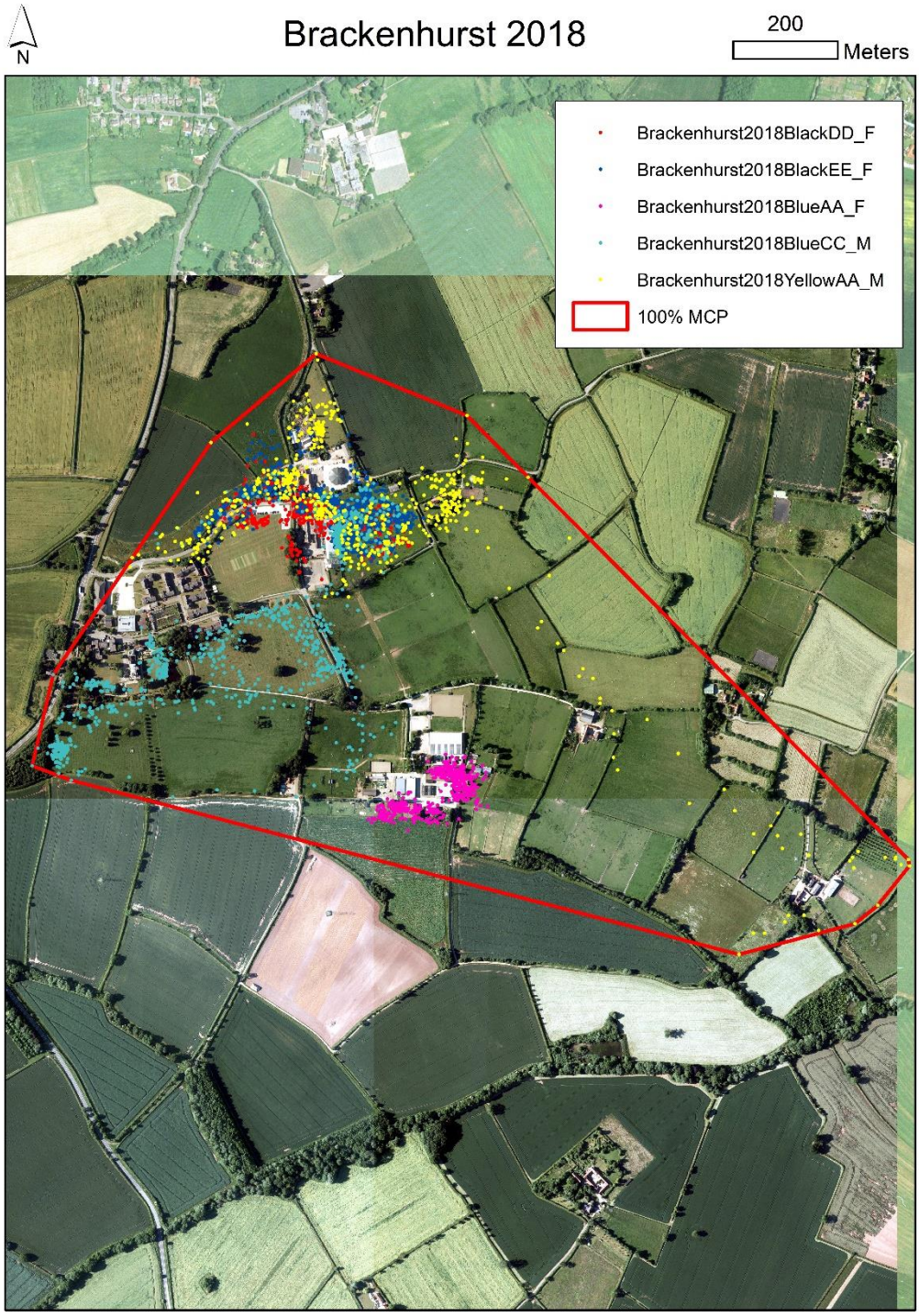



Figure C-8. Movement data of West European hedgehogs (*Erinaceus europaeus*) in Brackenhurst, 2018. Colours represent GPS fixes recorded by different individuals; red line represents the 100% Minimum Convex Polygon encompassing all GPS fixes recorded during the survey period.


Figure C-9. Movement data of West European hedgehogs (*Erinaceus europaeus*) in Sutton Bonington, 2018. Colours represent GPS fixes recorded by different individuals; red line represents the 100% Minimum Convex Polygon encompassing all GPS fixes recorded during the survey period.

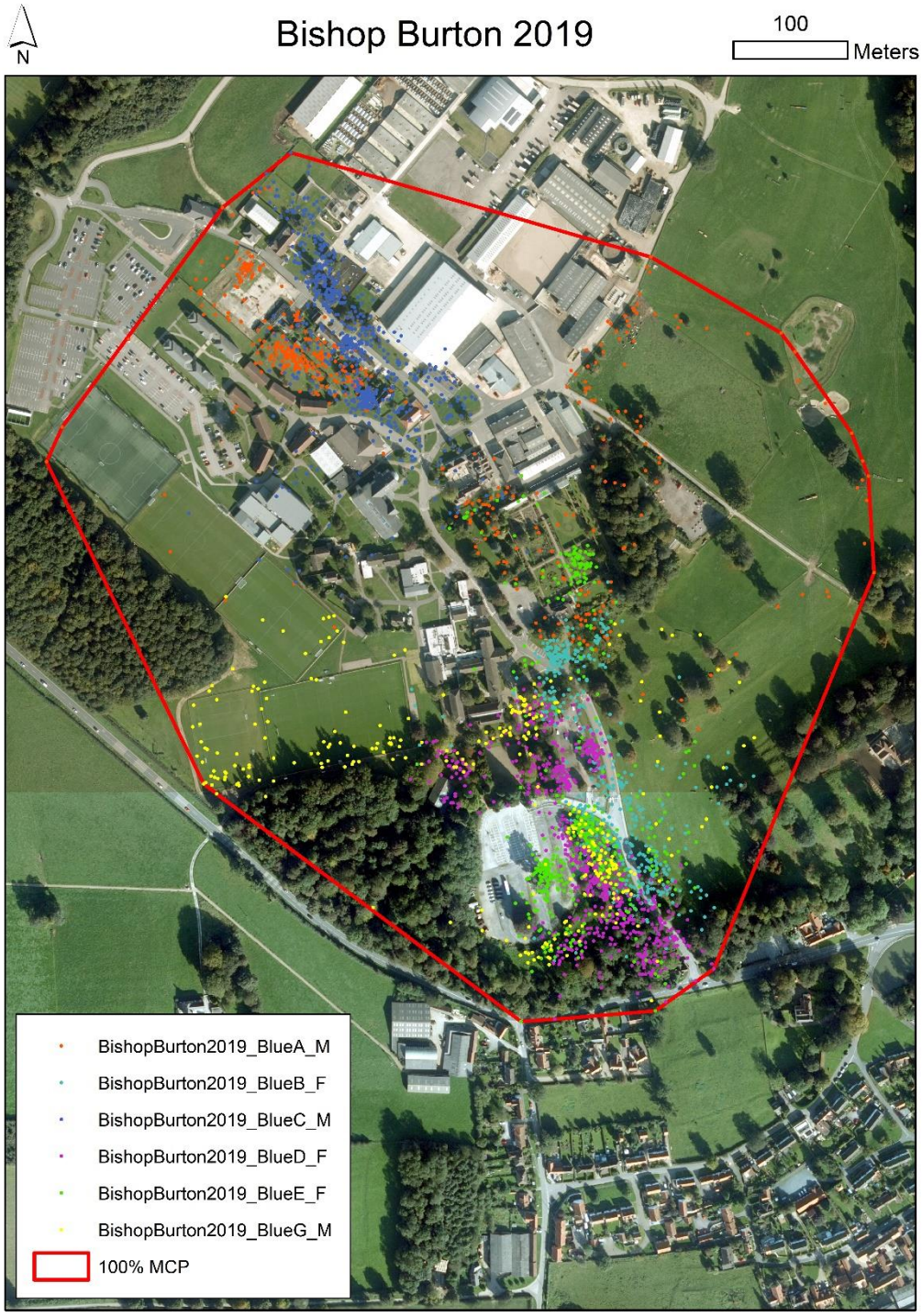



Figure C-10. Movement data of West European hedgehogs (*Erinaceus europaeus*) in Bishop Burton, 2019. Colours represent GPS fixes recorded by different individuals; red line represents the 100% Minimum Convex Polygon encompassing all GPS fixes recorded during the survey period.


Figure C-11. Movement data of West European hedgehogs (*Erinaceus europaeus*) in Riseholme, 2019. Colours represent GPS fixes recorded by different individuals; red line represents the 100% Minimum Convex Polygon encompassing all GPS fixes recorded during the survey period.

**Appendix D.** Maps representing the GPS fixes recorded by each individuals (n=52) across the urban and rural sites surveyed.

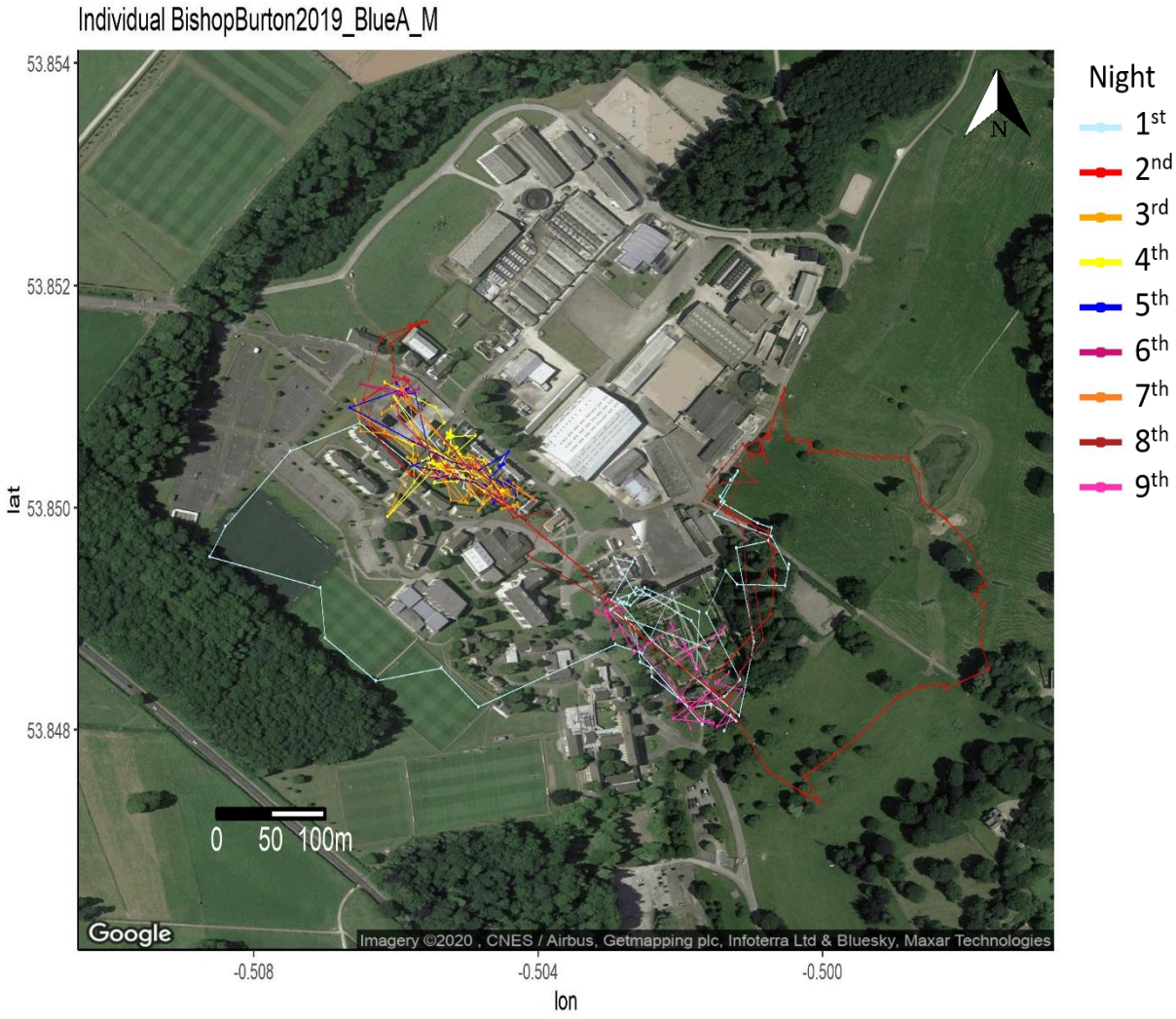



Figure D-1. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Bishop Burton (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

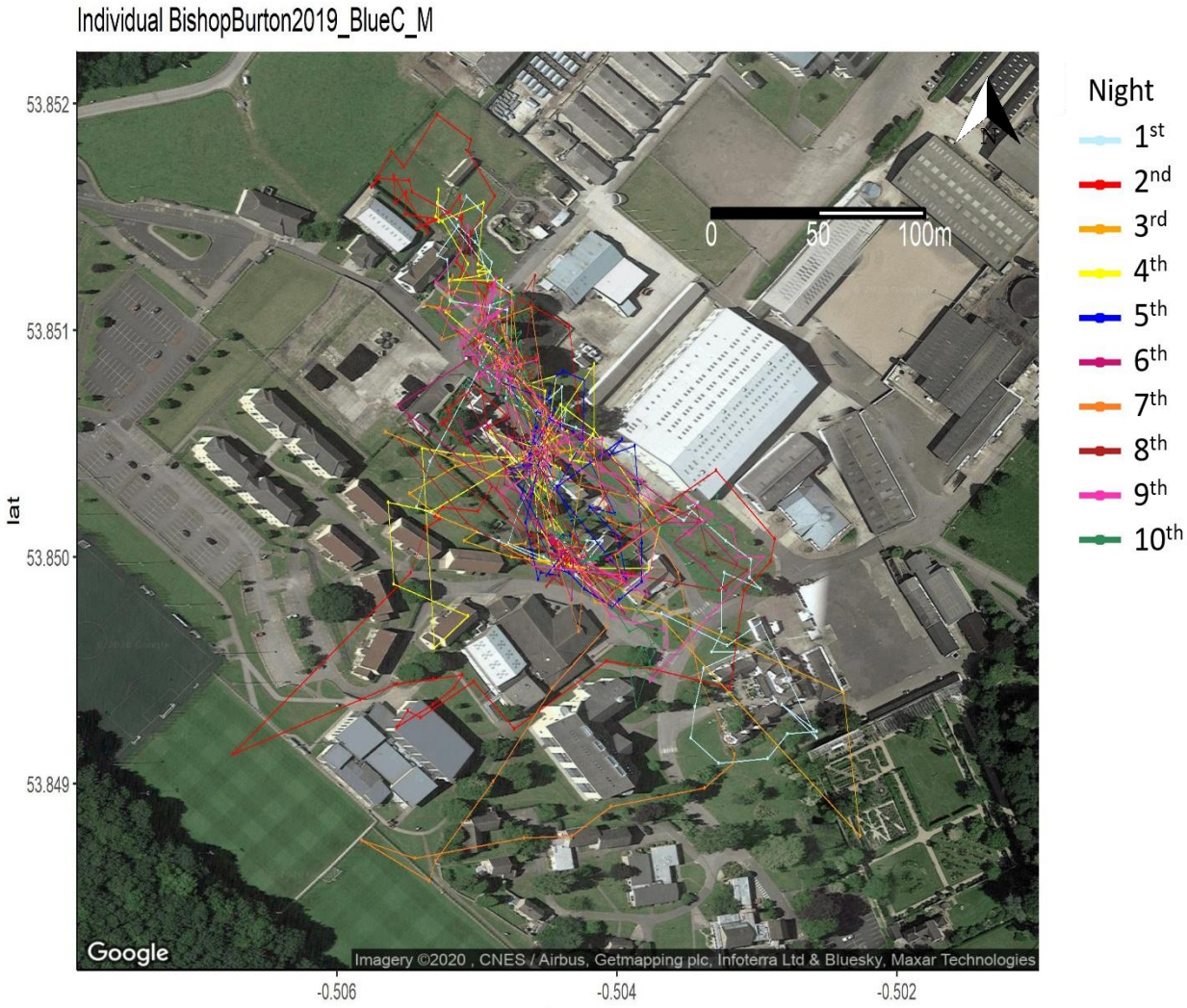



Figure D-2. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Bishop Burton (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

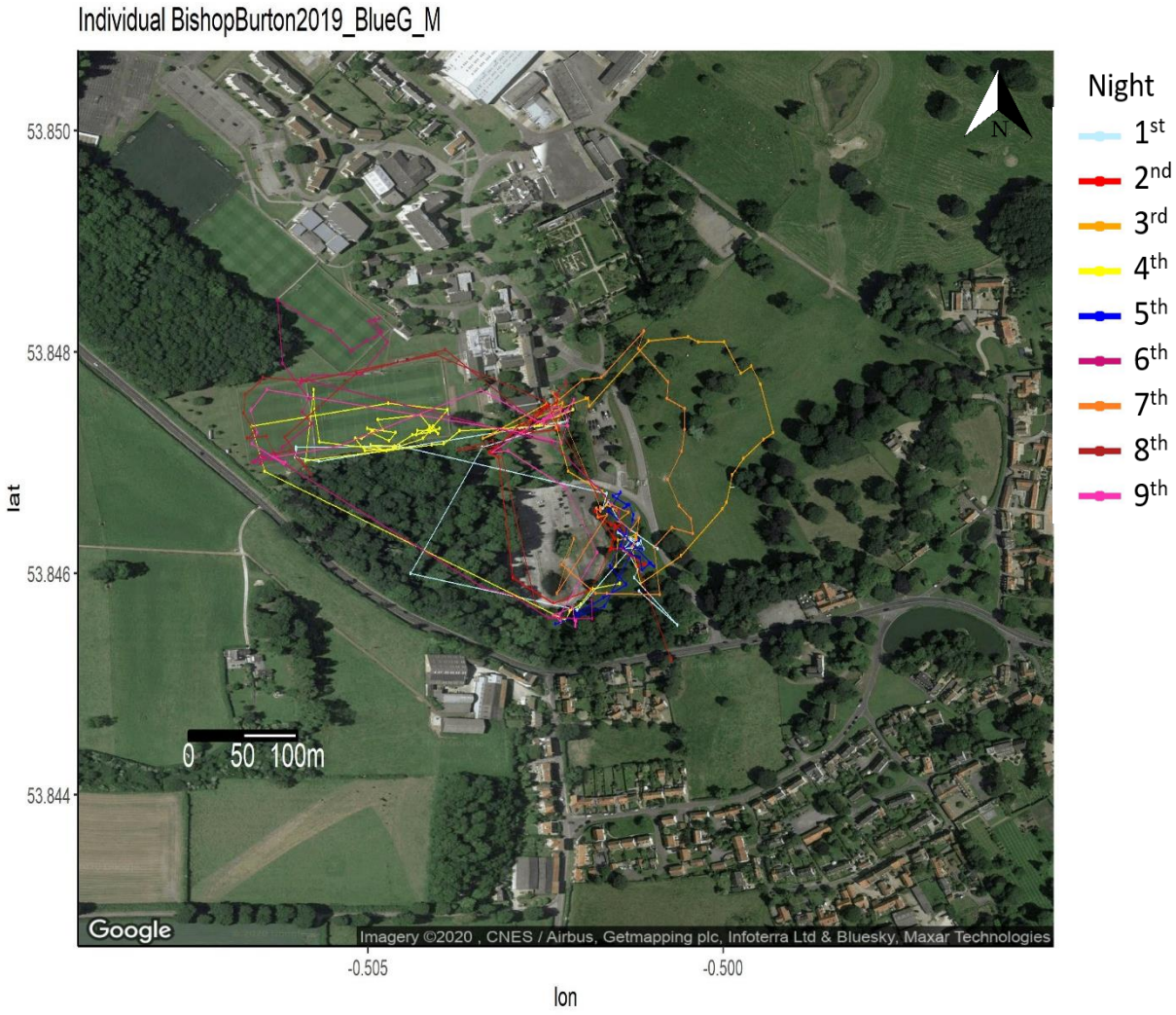



Figure D-3. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Bishop Burton (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

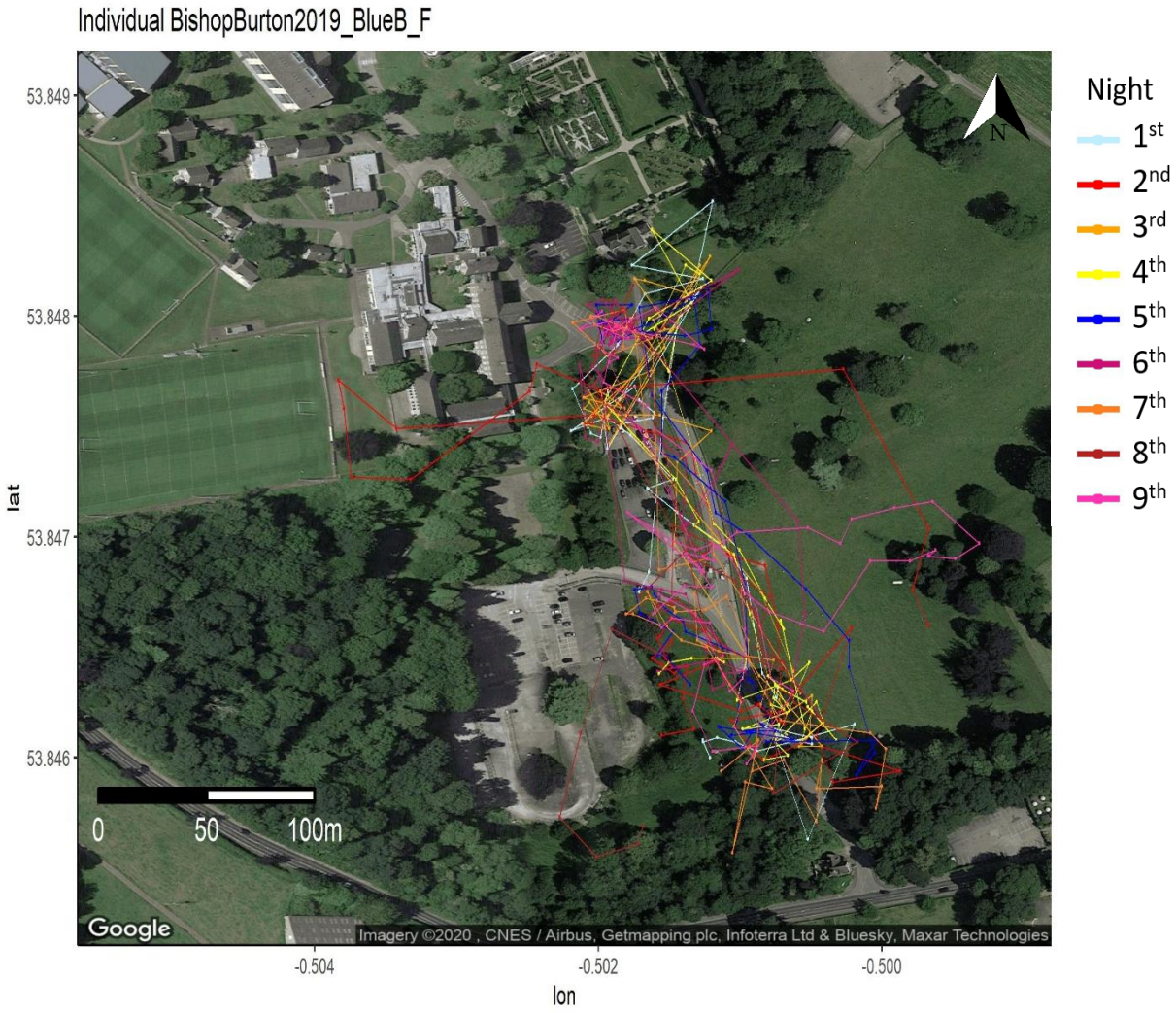



Figure D-4. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Bishop Burton (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

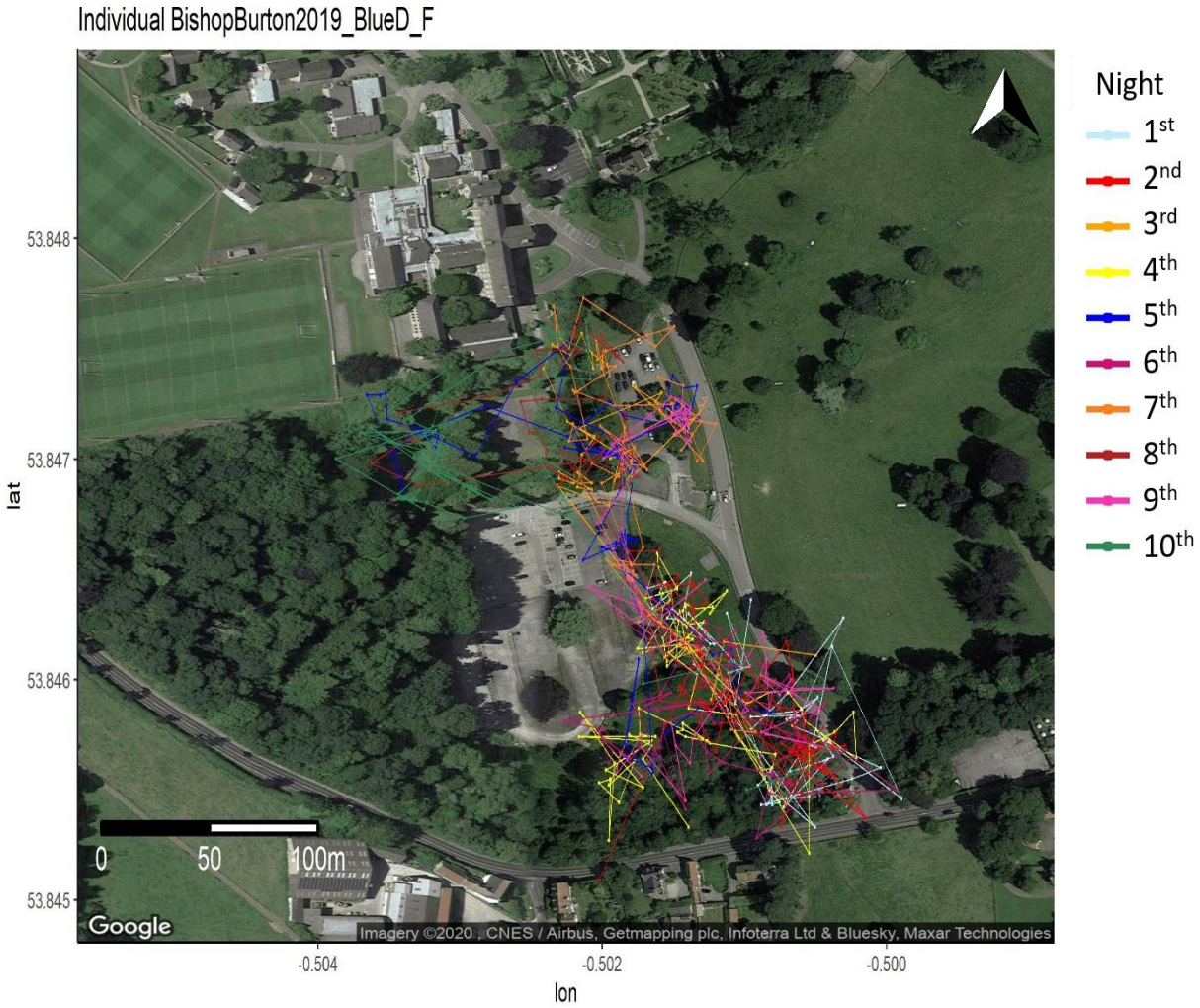



Figure D-5. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Bishop Burton (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

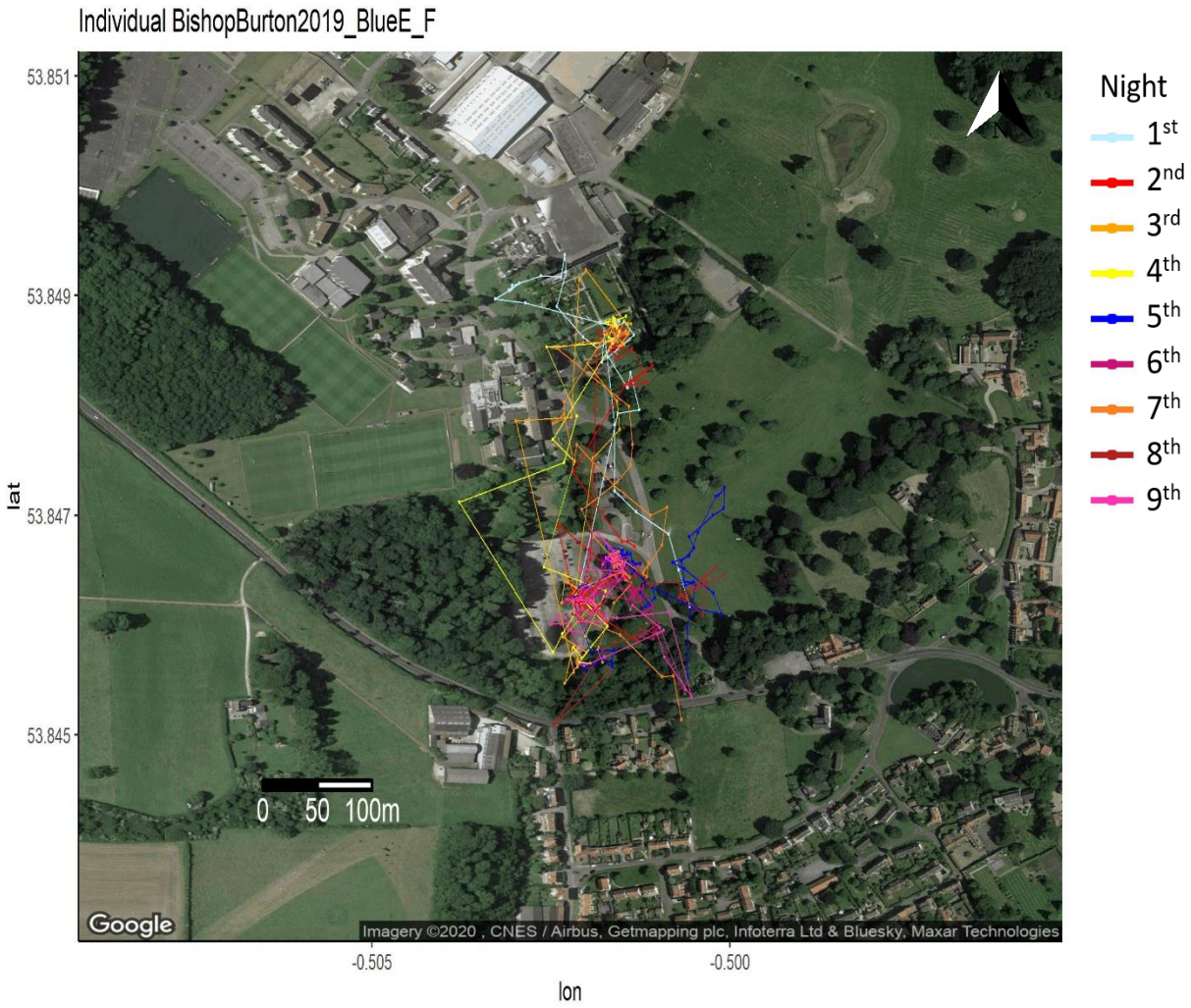



Figure D-6. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Bishop Burton (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).


Figure D-7. Movement data of a male rural hedgehog (*Erinaceus europaeus*) at Brackenhurst 2017 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).


Figure D-8. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Brackenhurst 2017 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

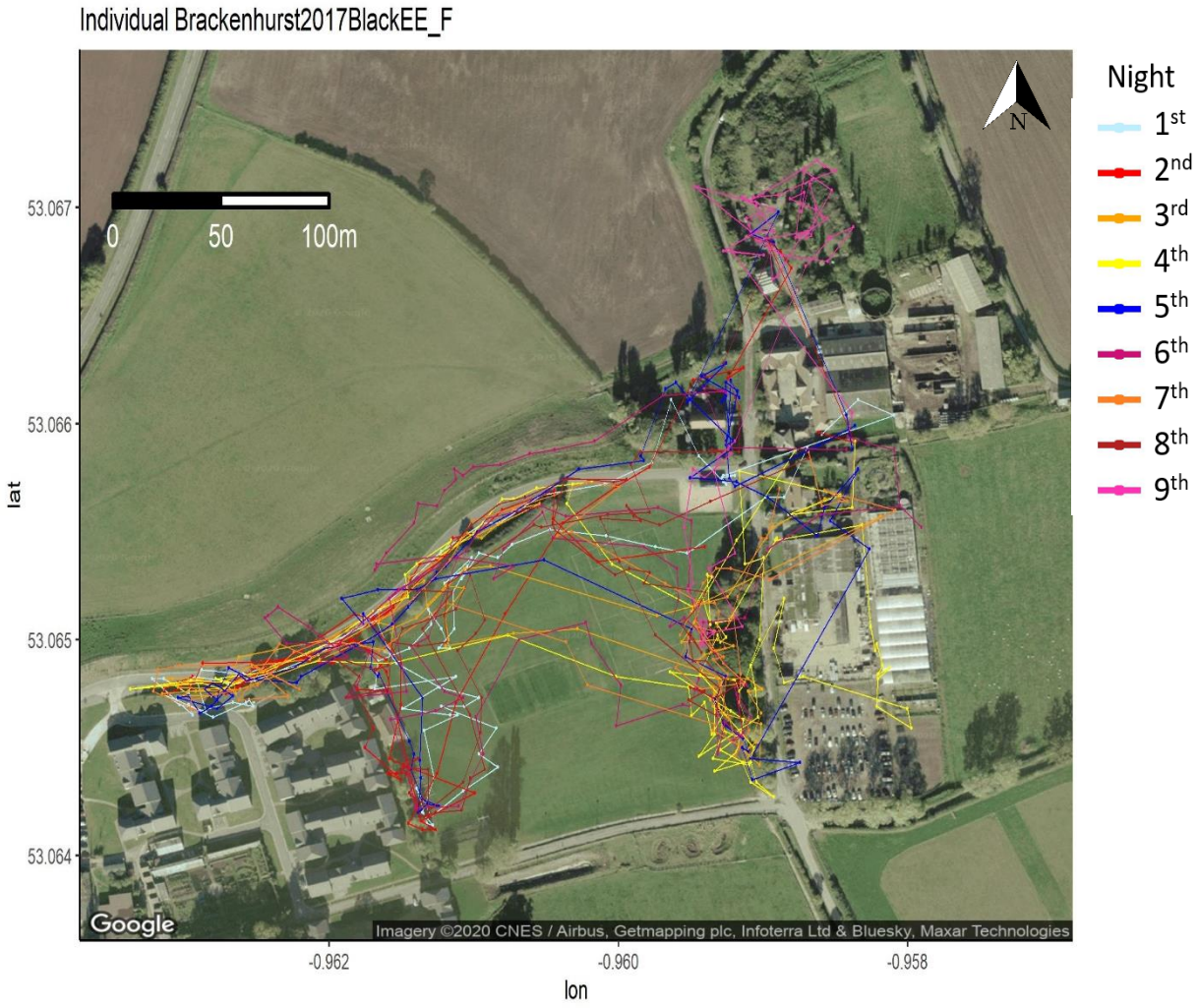



Figure D-9. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Brackenhurst 2017 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

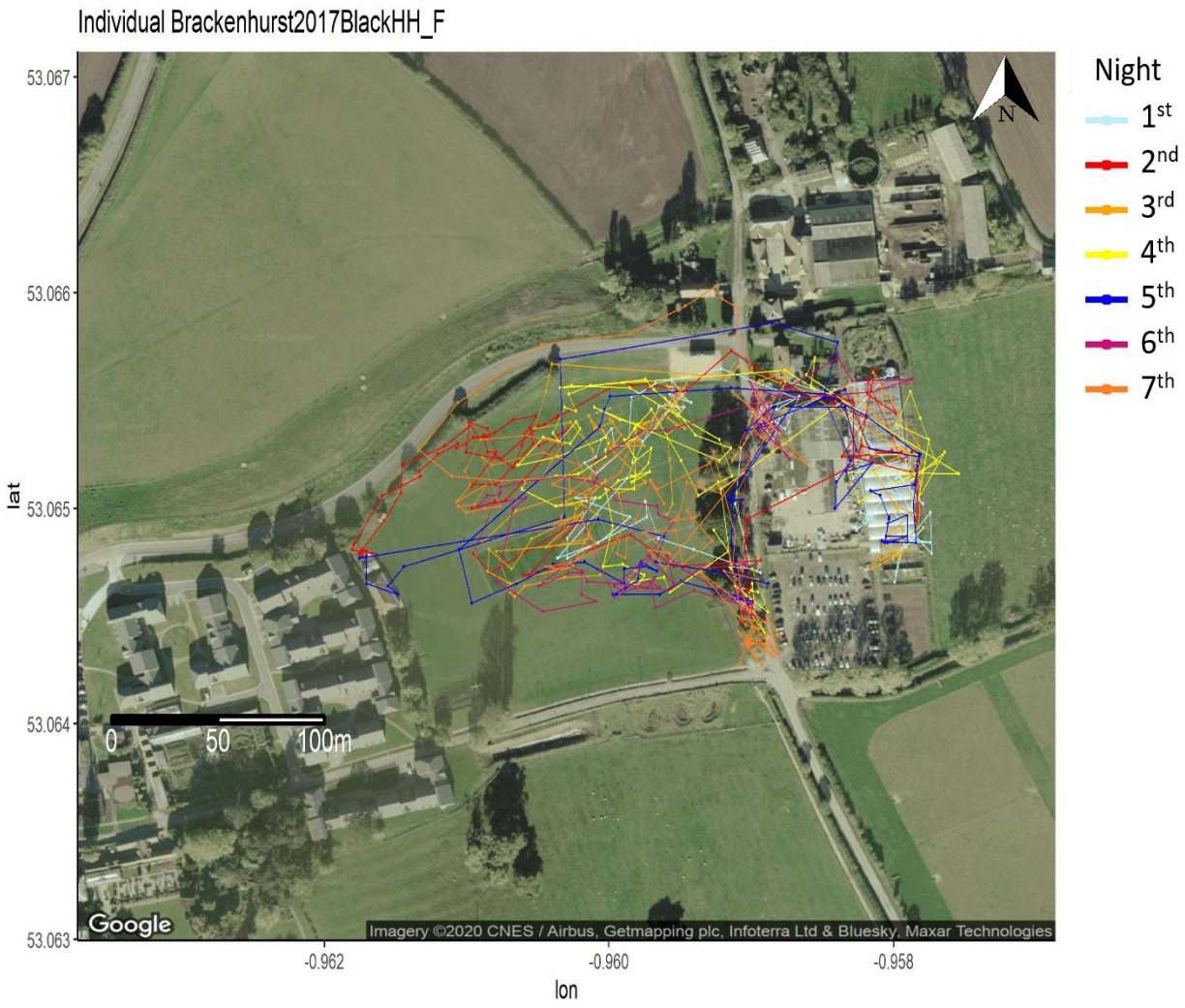



Figure D-10. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Brackenhurst 2017 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

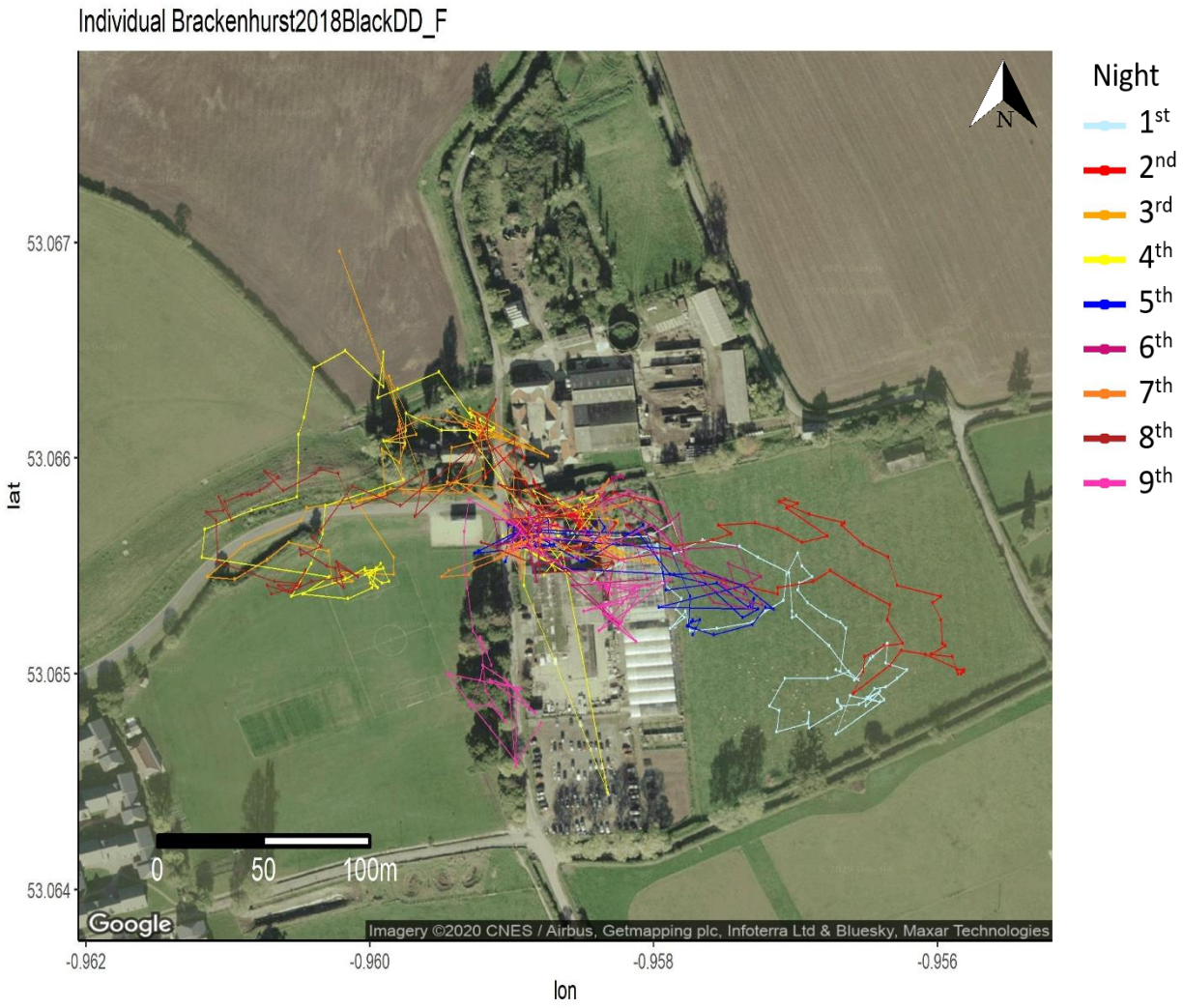



Figure D-11. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Brackenhurst 2018 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

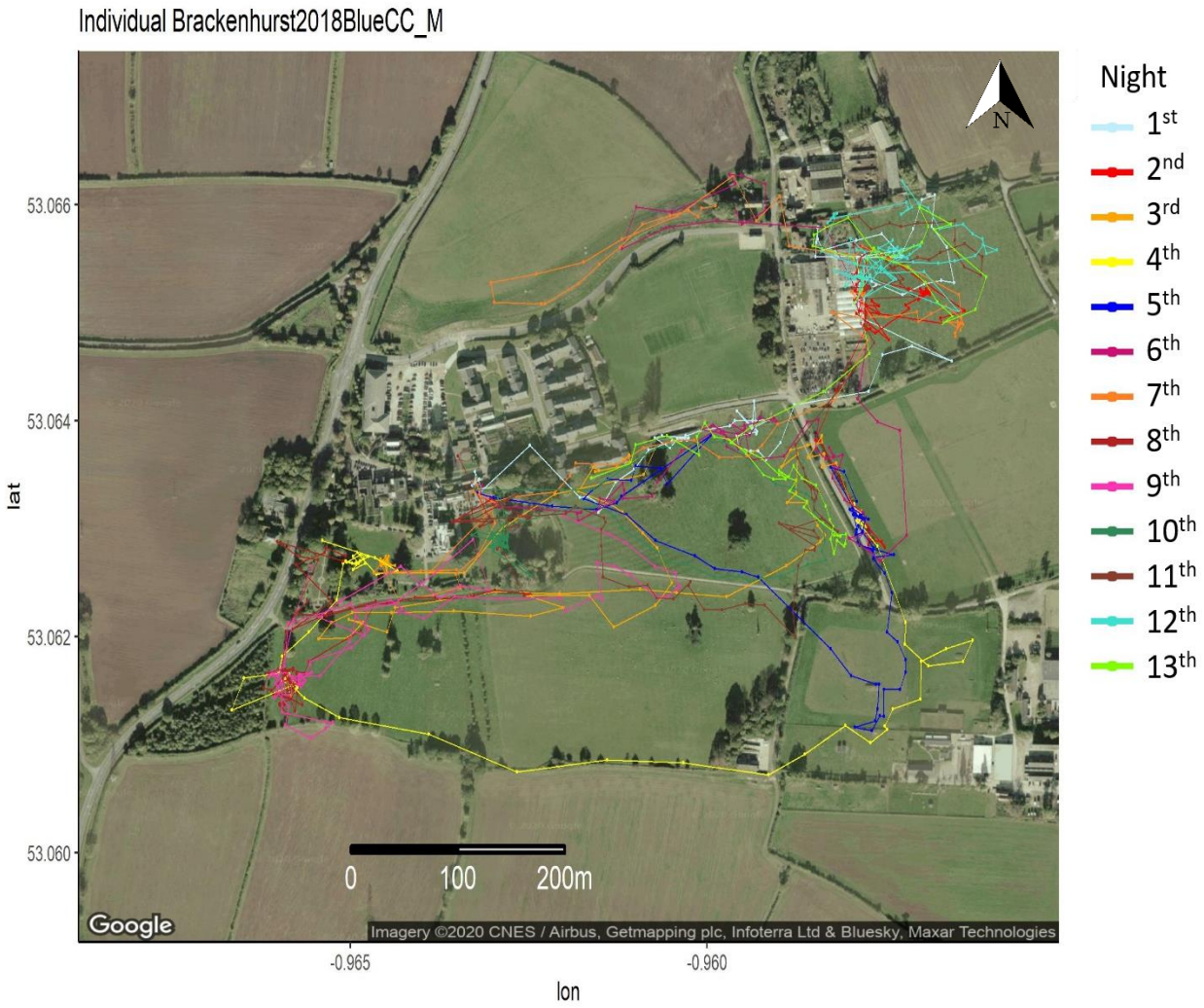



Figure D-12. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Brackenhurst 2018 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).


Figure D-13. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Brackenhurst 2018 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).


Figure D-14. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Brackenhurst 2018 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).


Figure D-15. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Brackenhurst 2018 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

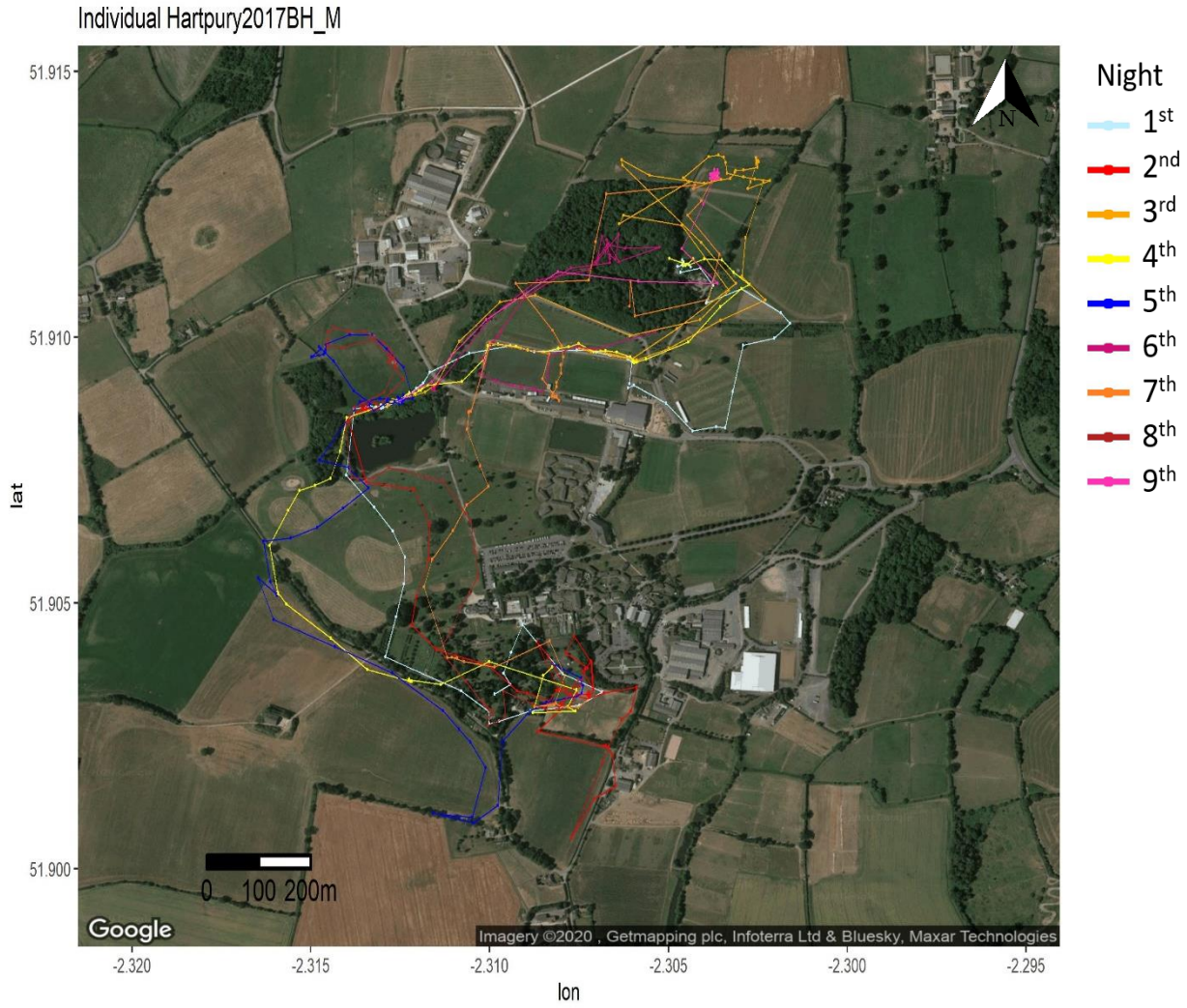



Figure D-16. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Hartpury 2017 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

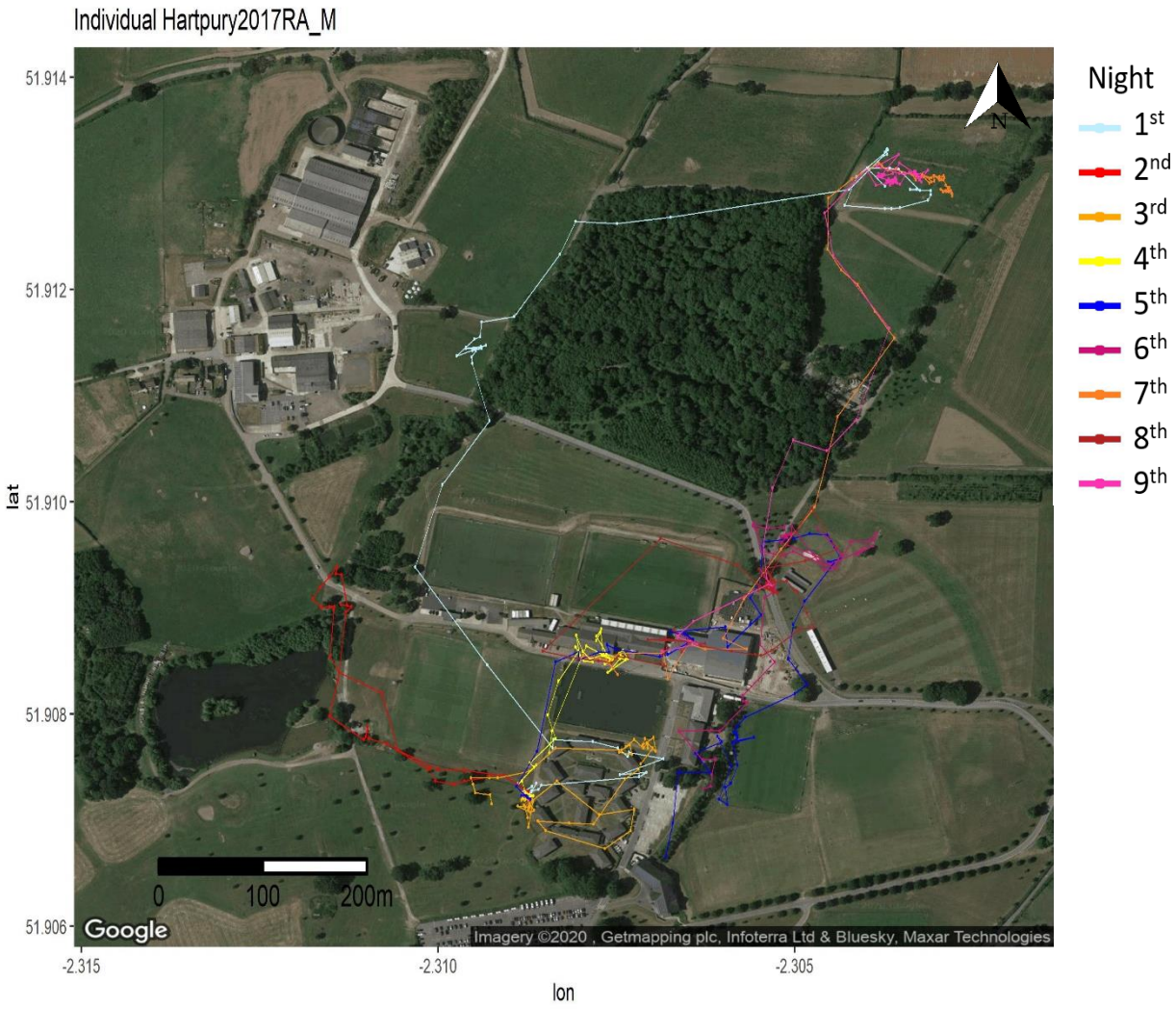



Figure D-17. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Hartpury 2017 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

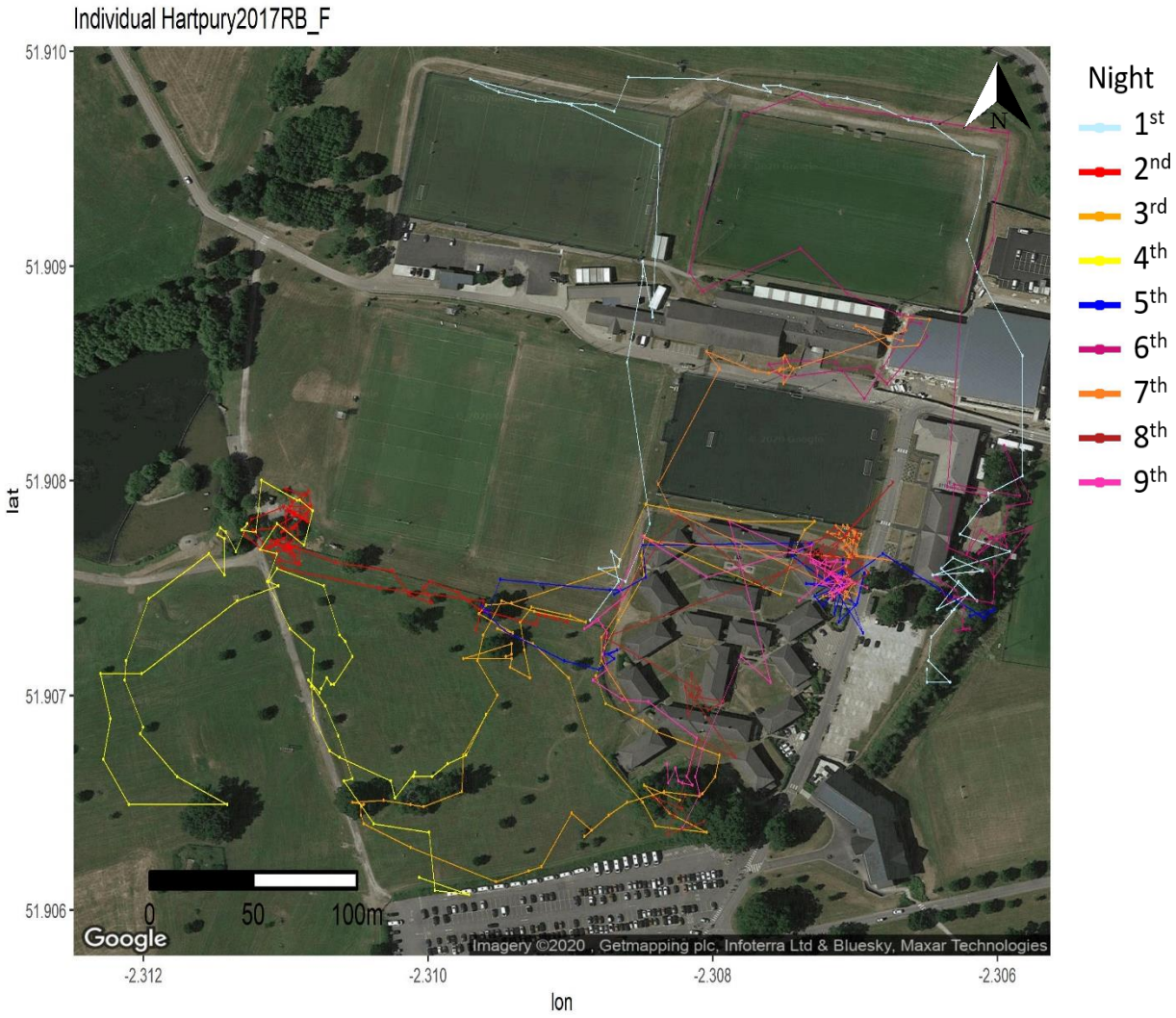



Figure D-18. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Hartpury 2017 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

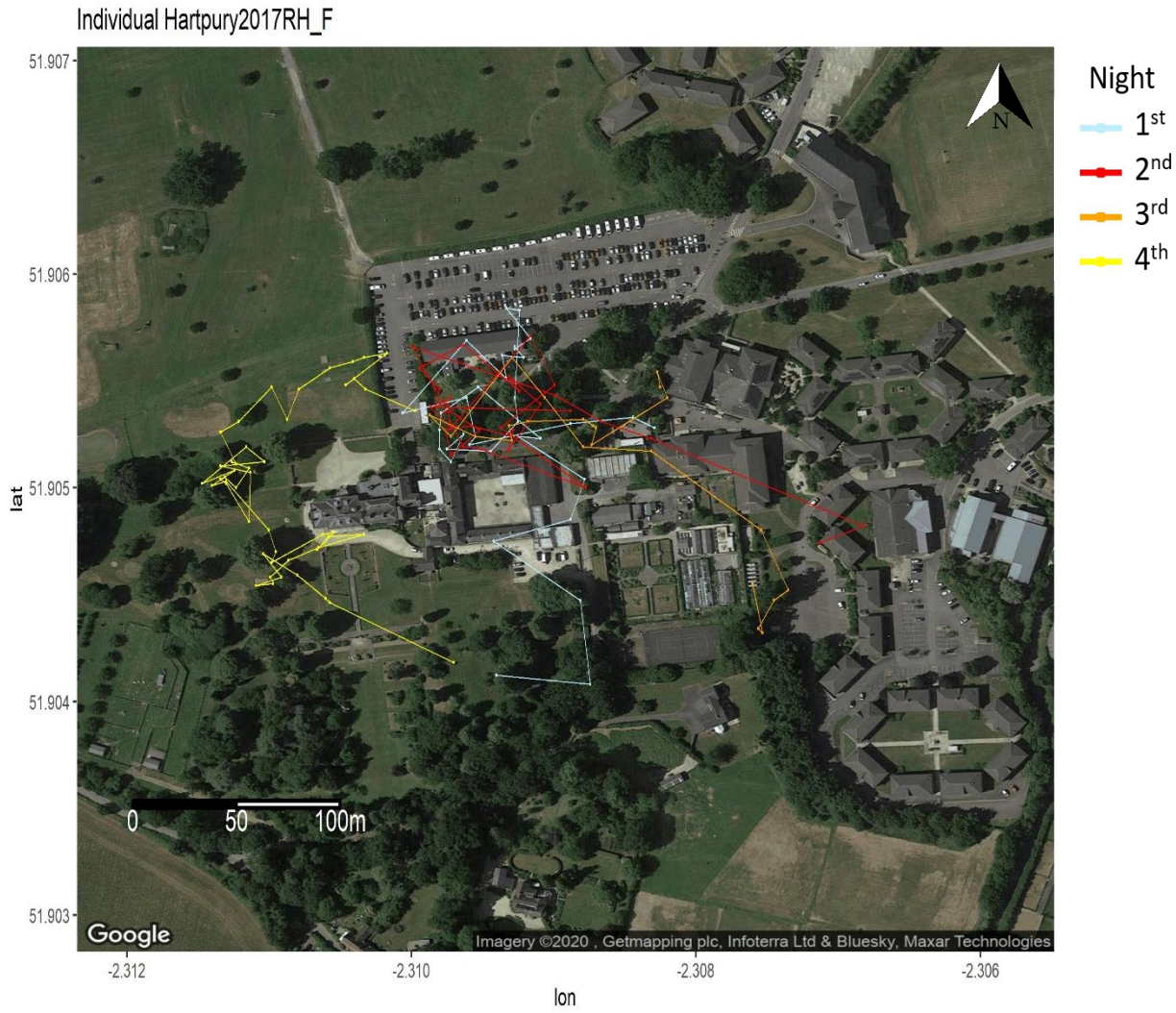



Figure D-19. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Hartpury 2017 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

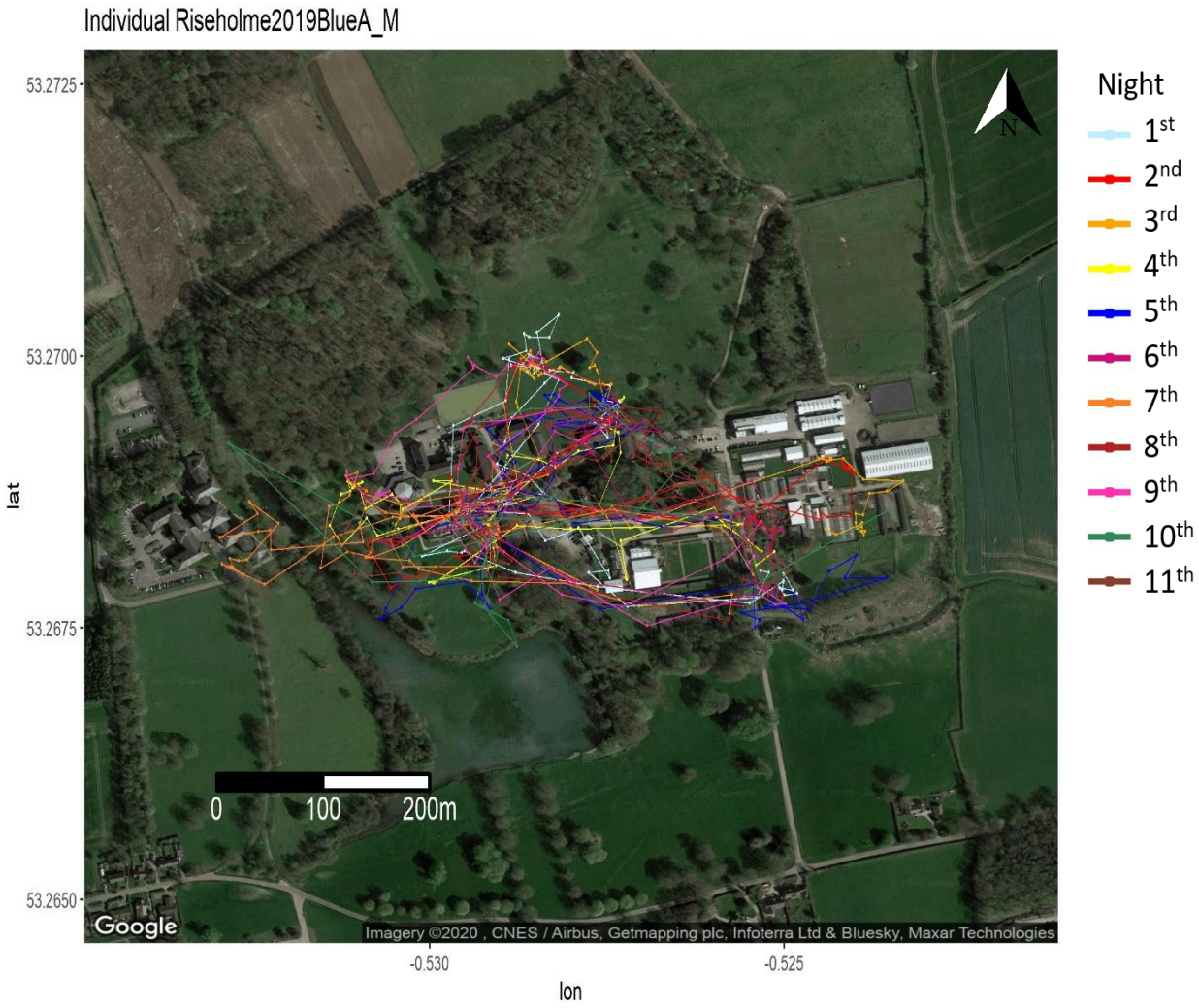



Figure D-20. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Riseholme 2019 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).


Figure D-21. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Riseholme 2019 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

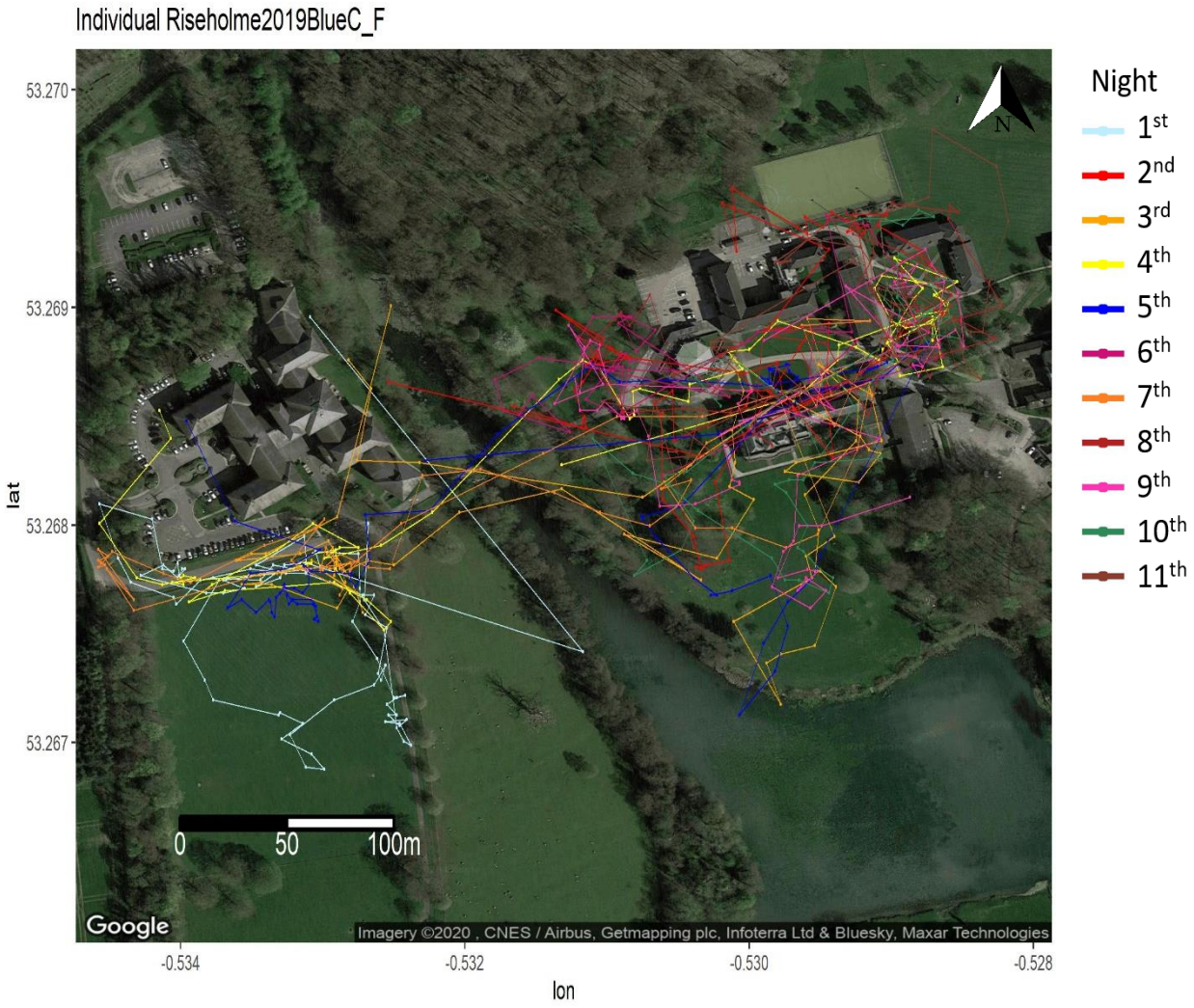



Figure D-22. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Riseholme 2019 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

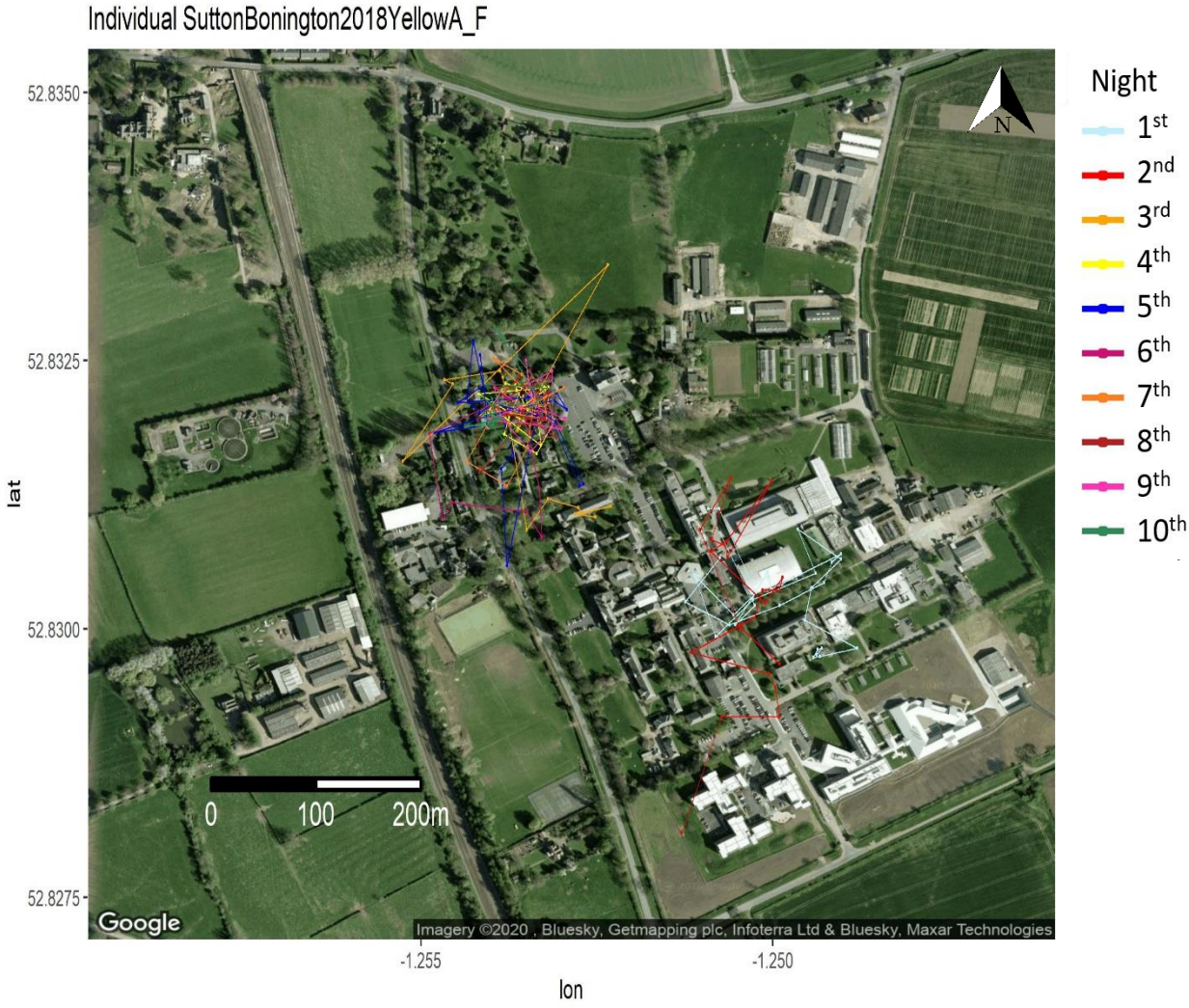



Figure D-23. Movement data of a male rural West European hedgehog (*Erinaceus europaeus*) at Sutton Bonington 2018 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

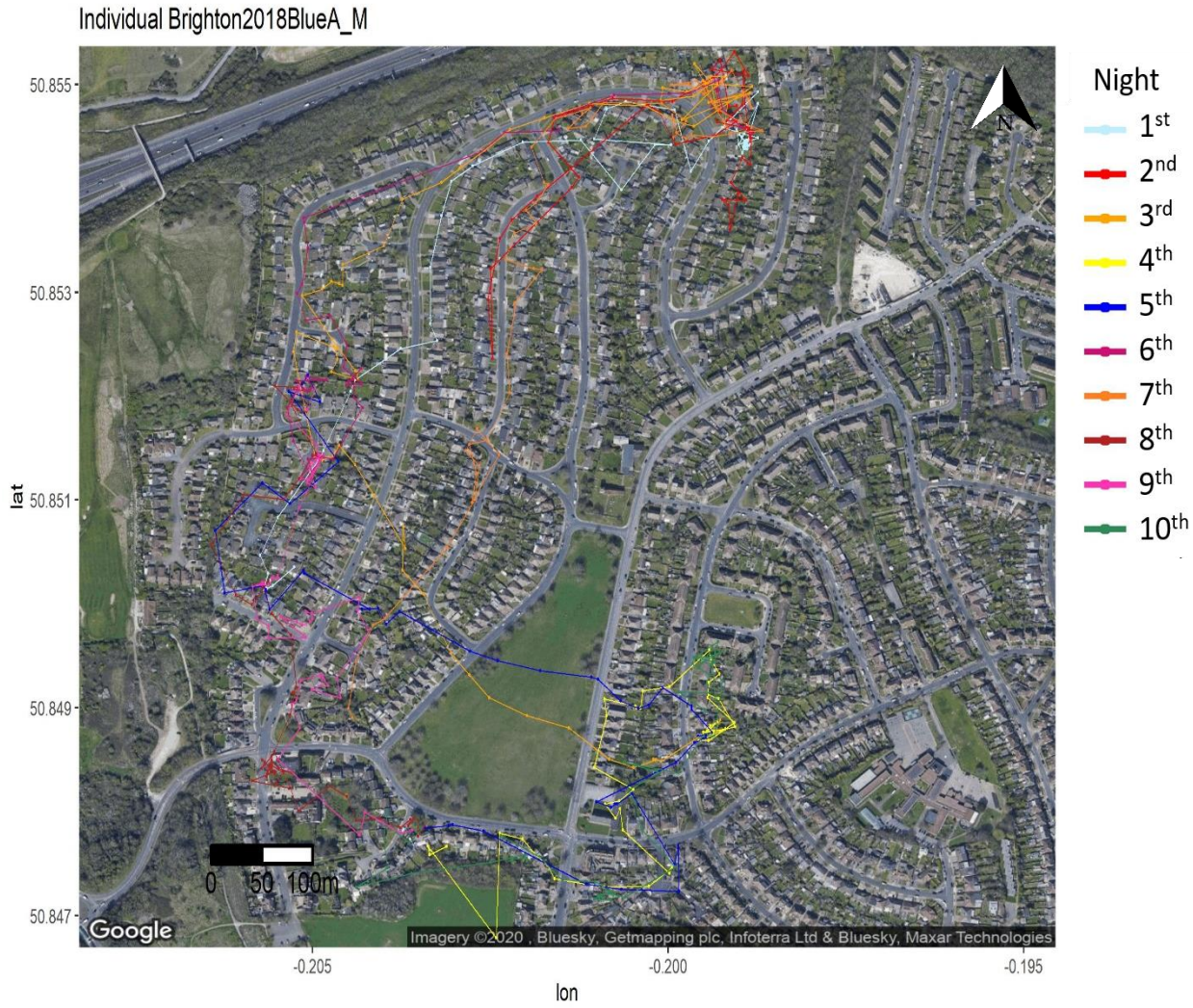



Figure D-24. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Brighton 2018 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).


Figure D-25. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Brighton 2018 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

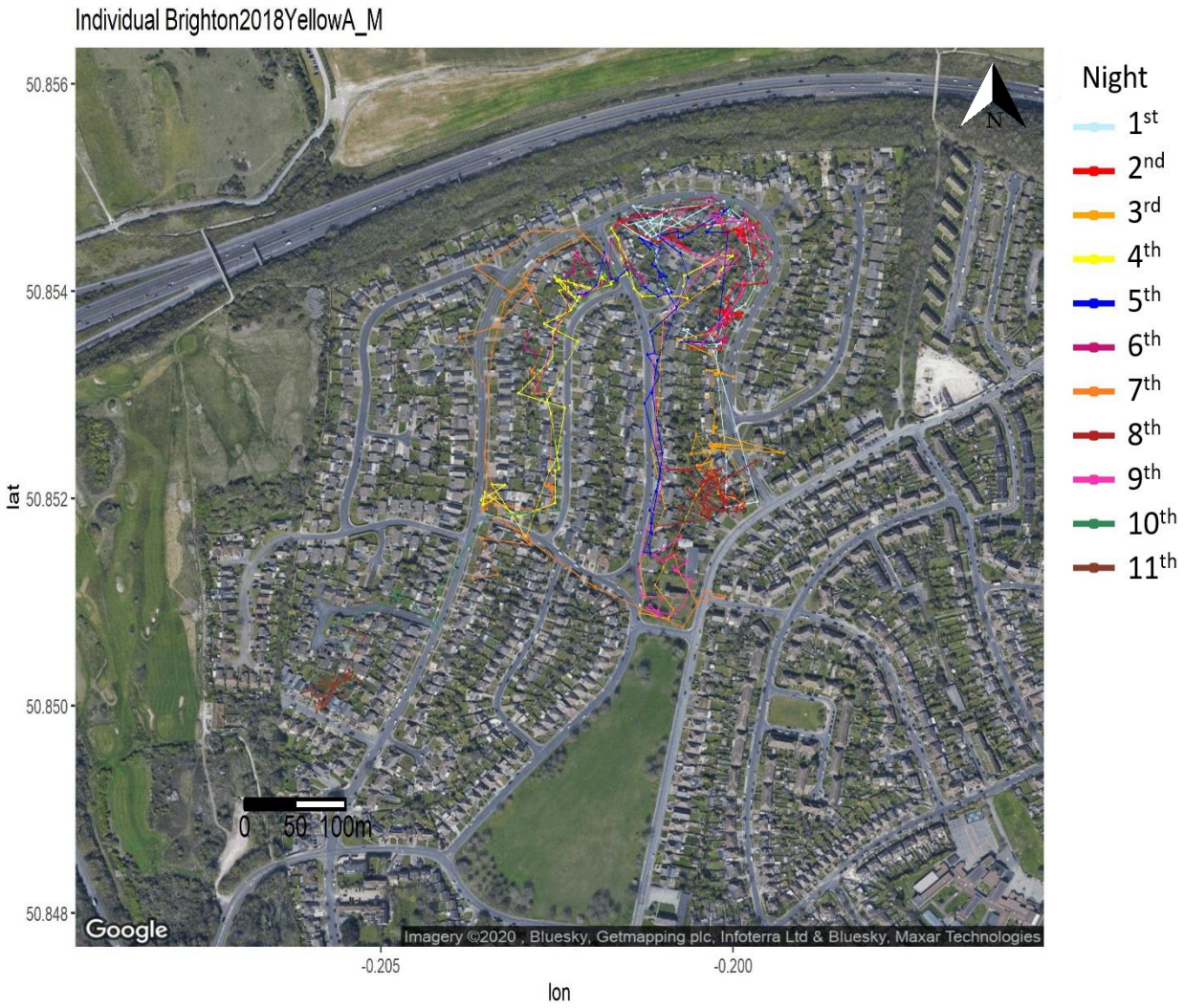



Figure D-26. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Brighton 2018 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

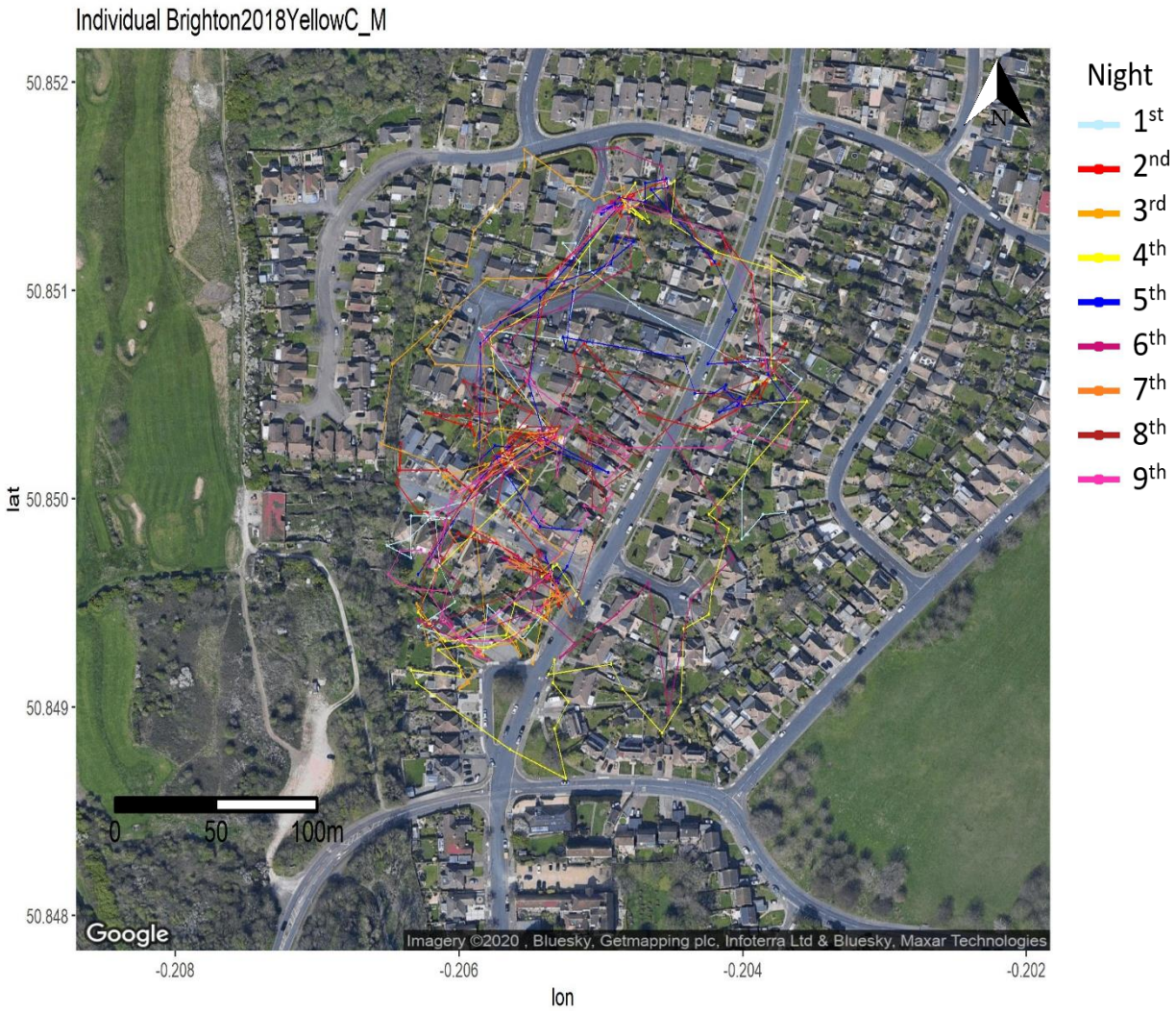



Figure D-27. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Brighton 2018 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

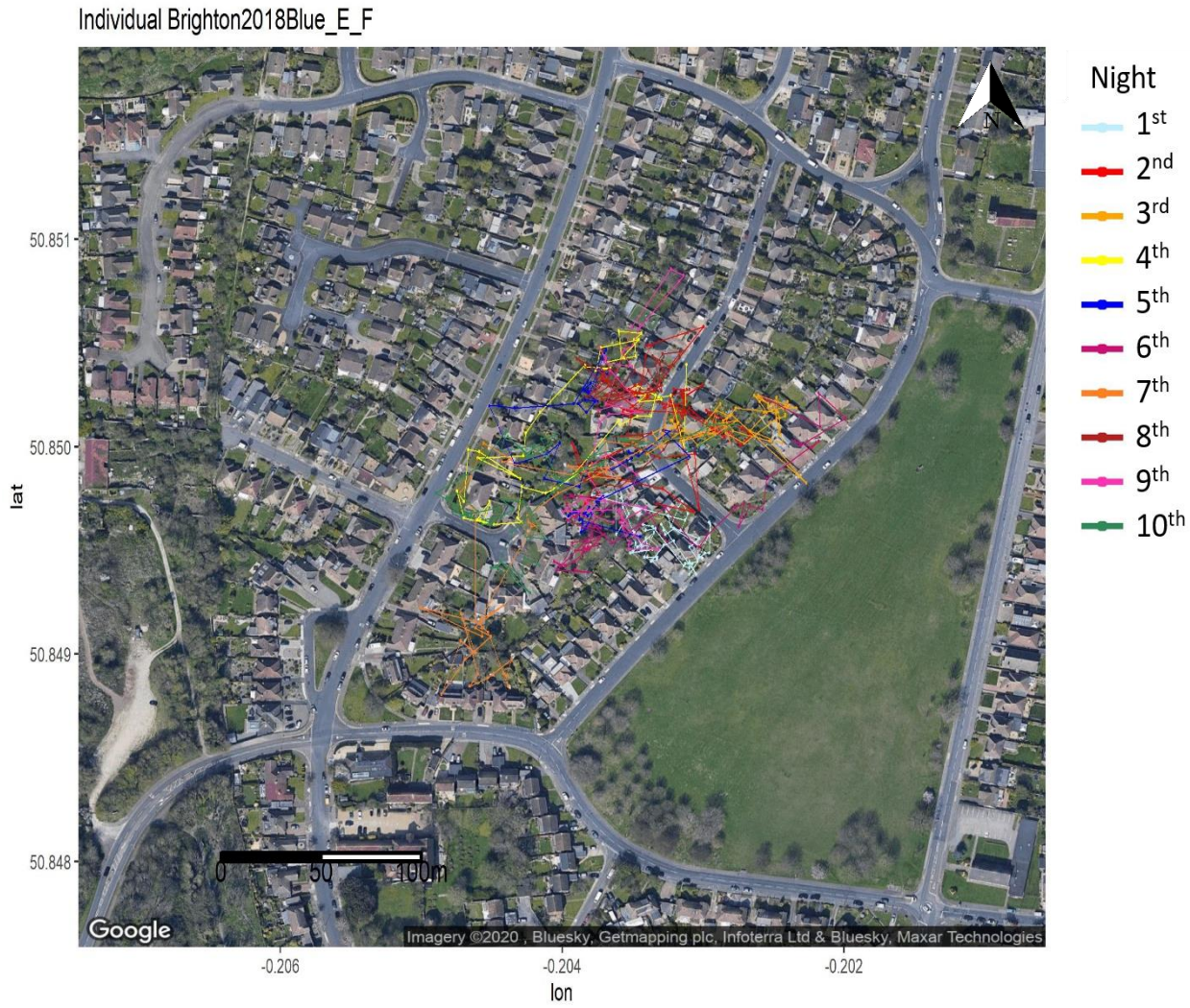



Figure D-28. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Brighton 2018 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

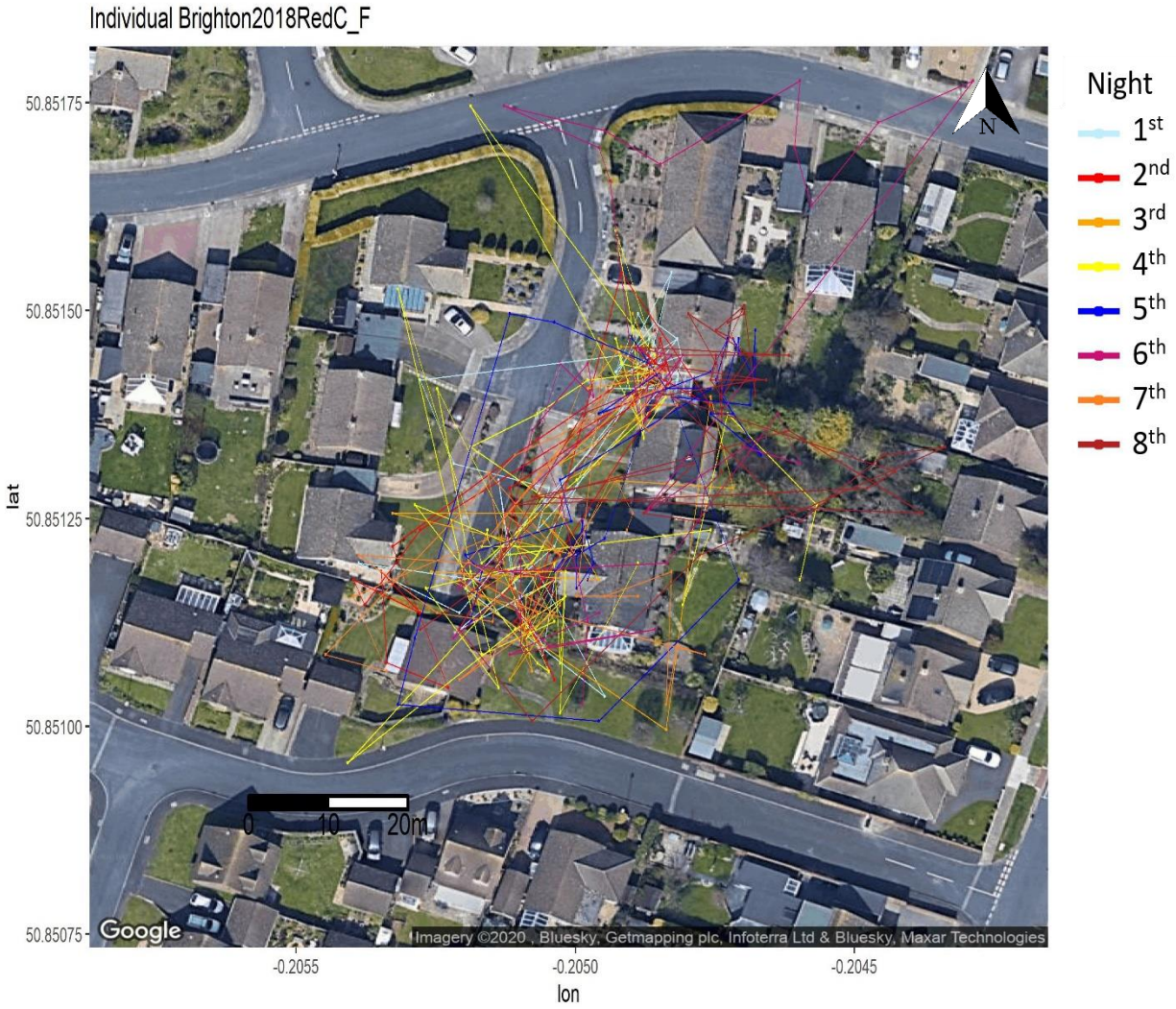



Figure D-29. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Brighton 2018 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

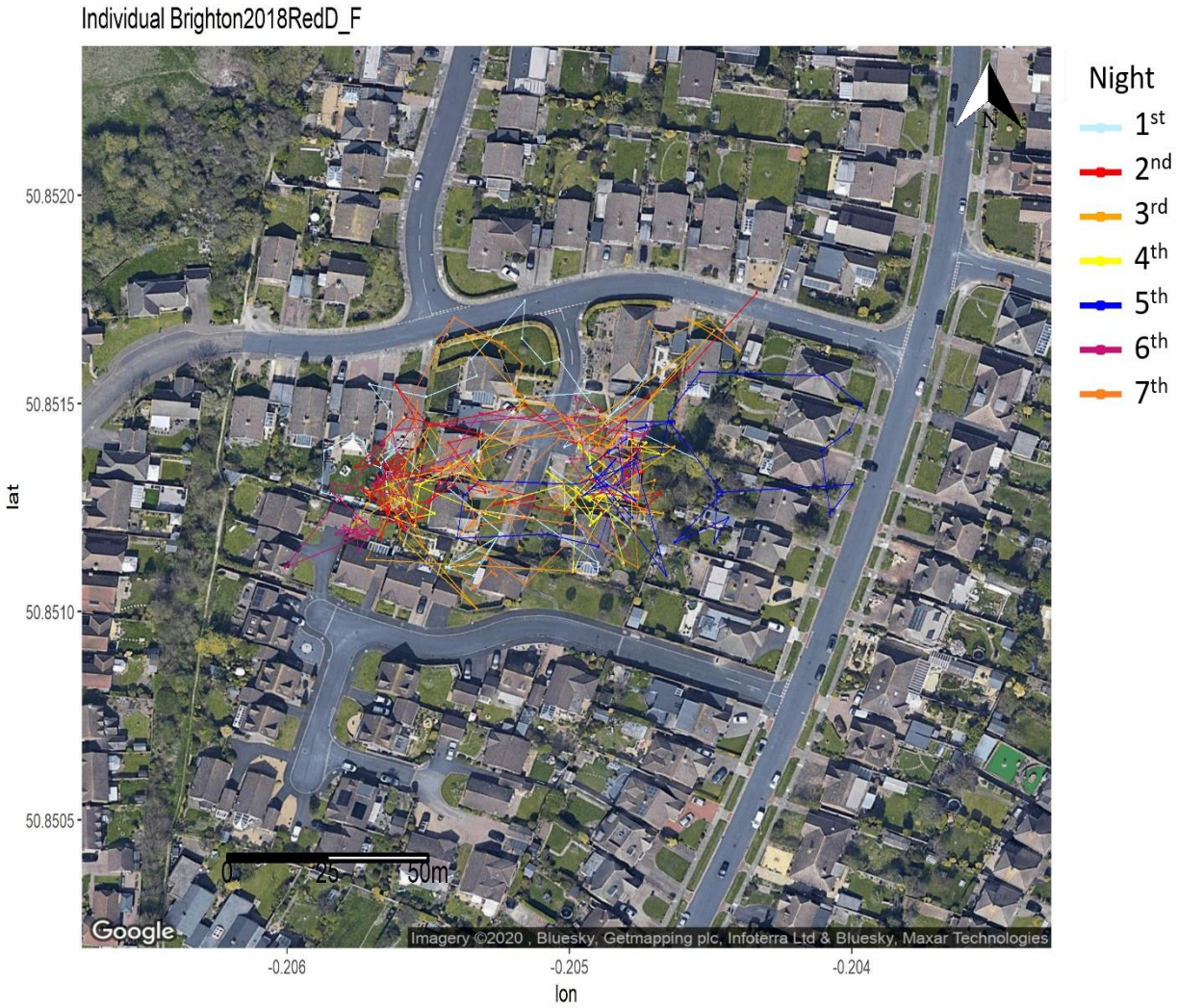



Figure D-30. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Brighton 2018 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

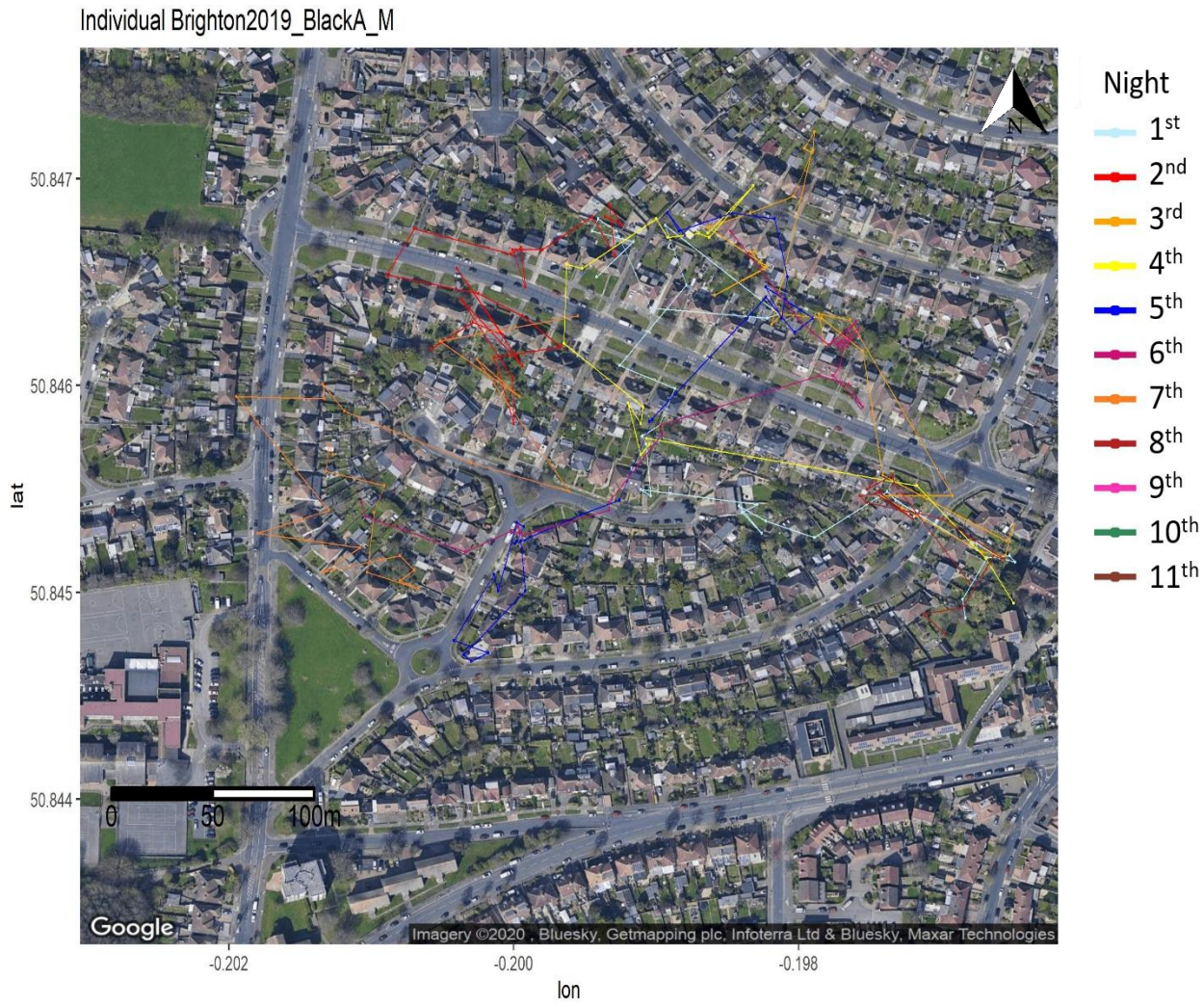



Figure D-31. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Brighton 2019 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).


Figure D-32. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Brighton 2019 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).


Figure D-33. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Brighton 2019 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

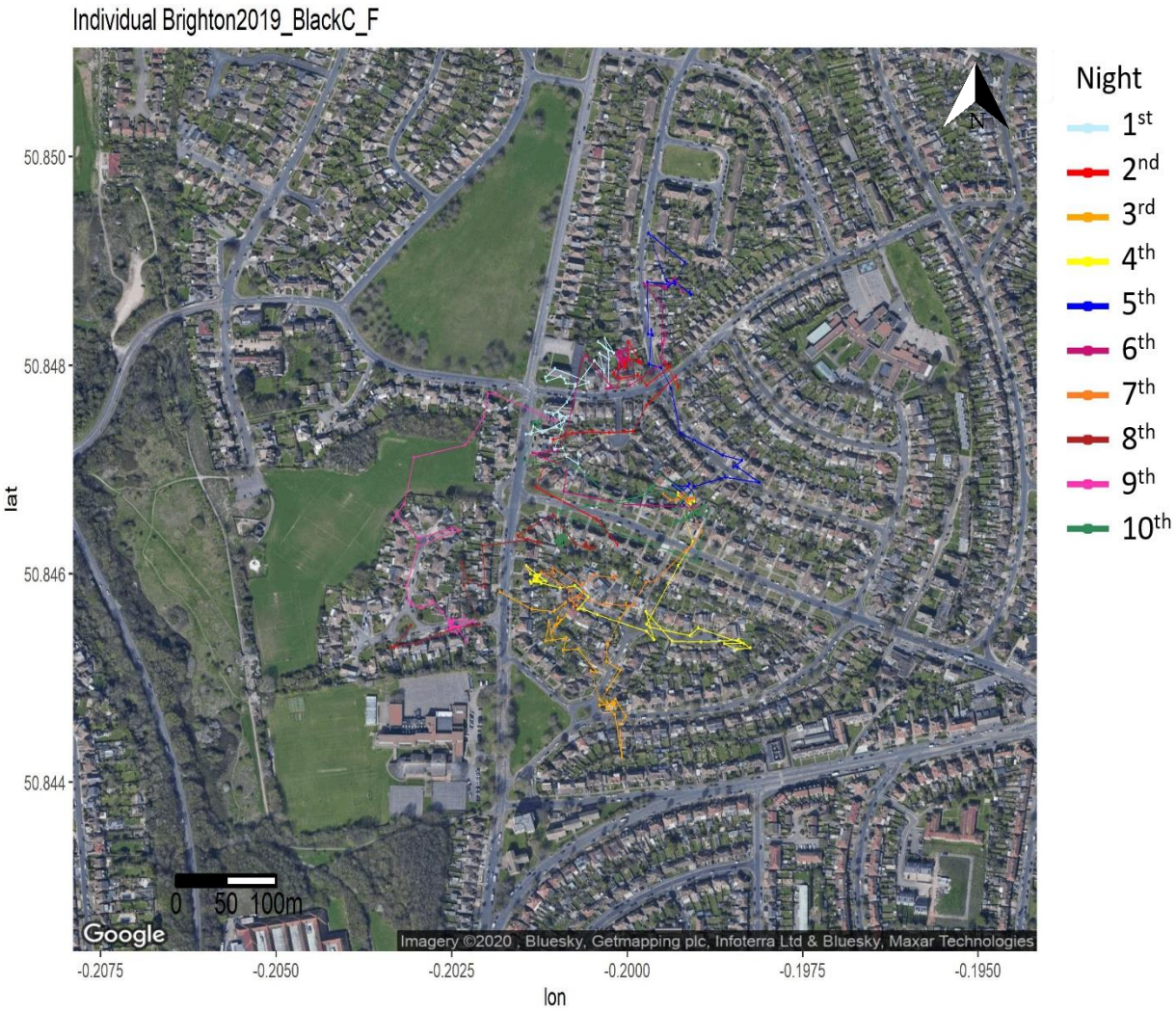



Figure D-34. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Brighton 2019 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

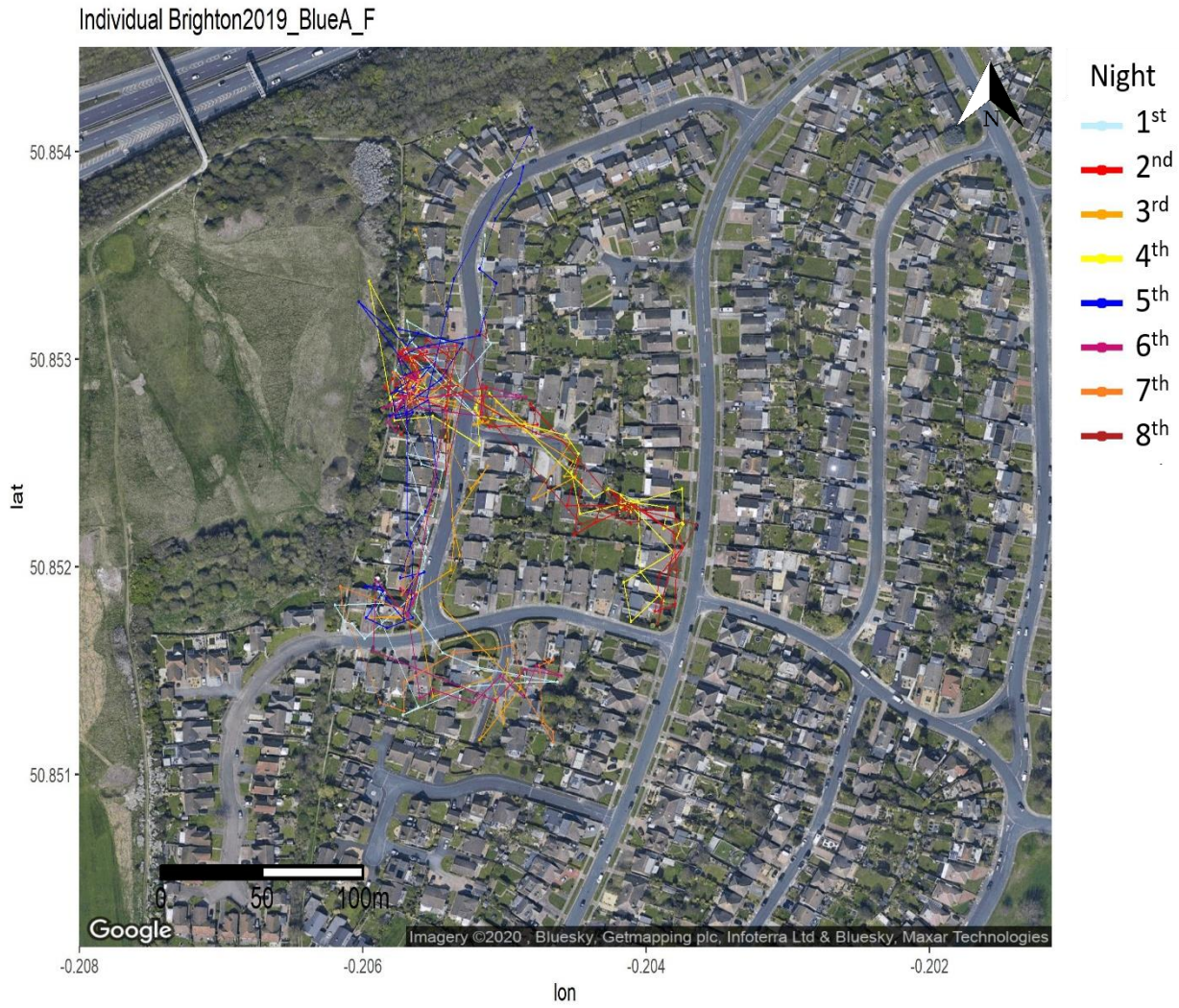



Figure D-35. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Brighton 2019 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).


Figure D-36. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Brighton 2019 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).


Figure D-37. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Ipswich West 2017 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

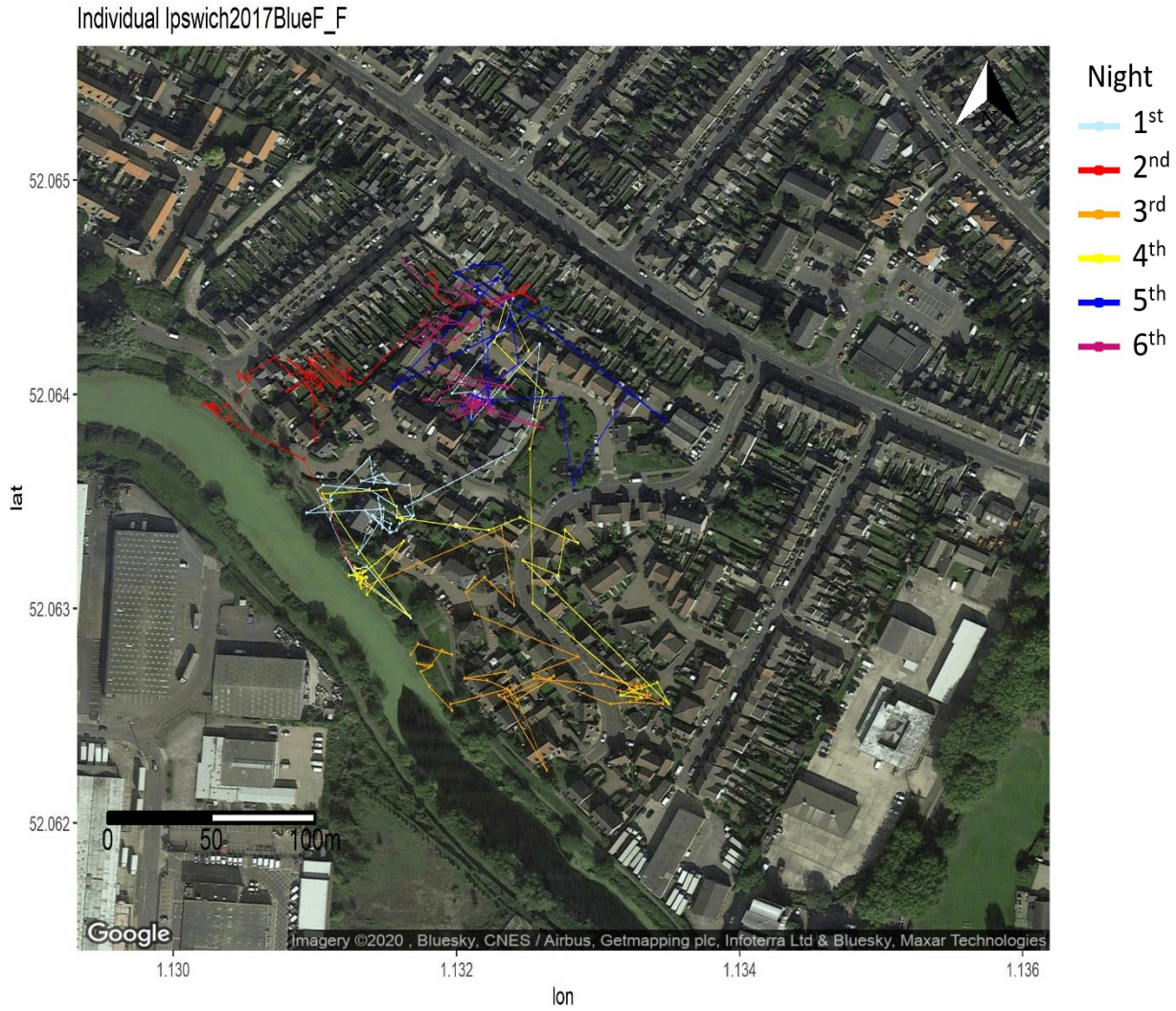



Figure D-38. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Ipswich West 2017 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

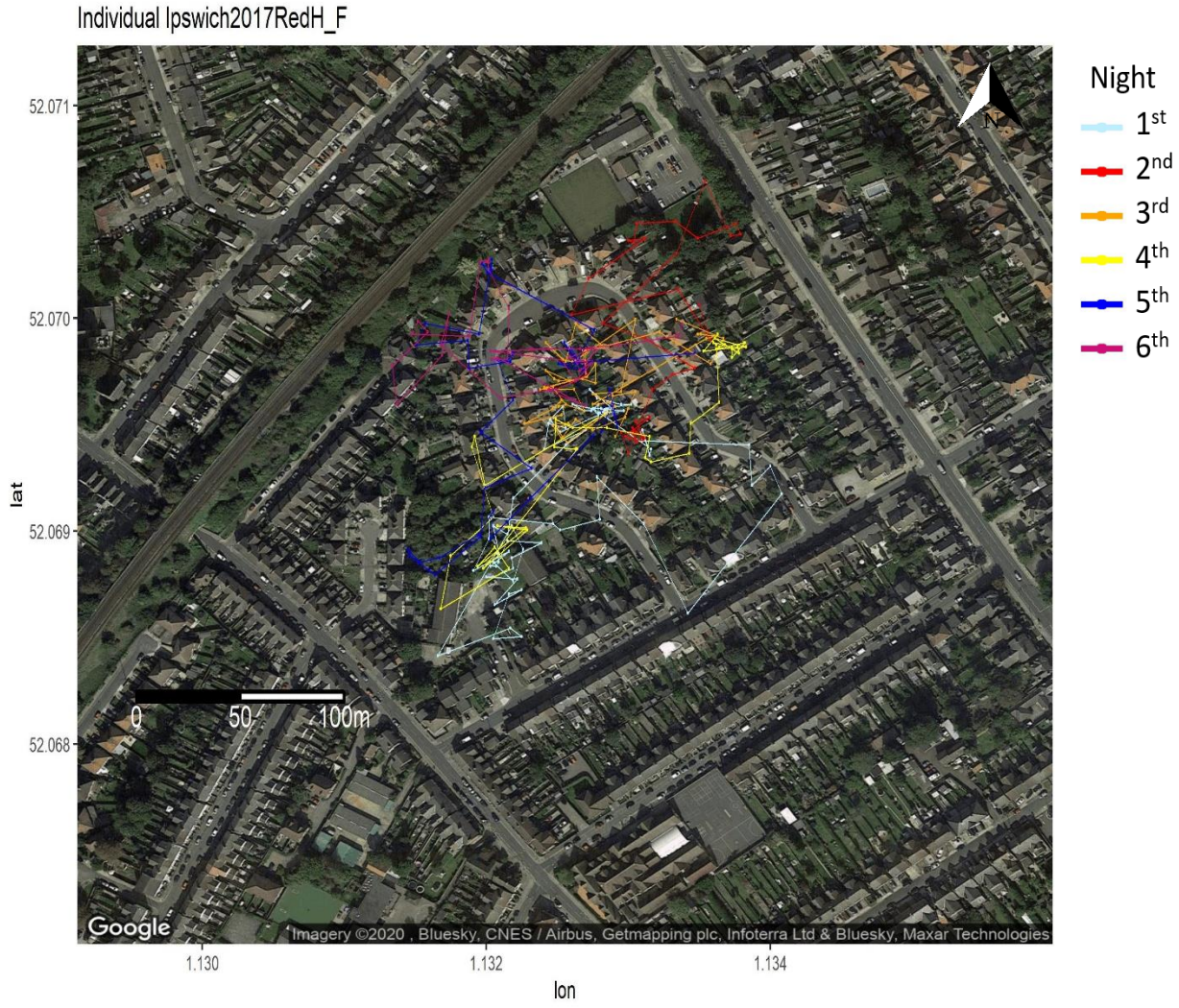



Figure D-39. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Ipswich West 2017 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

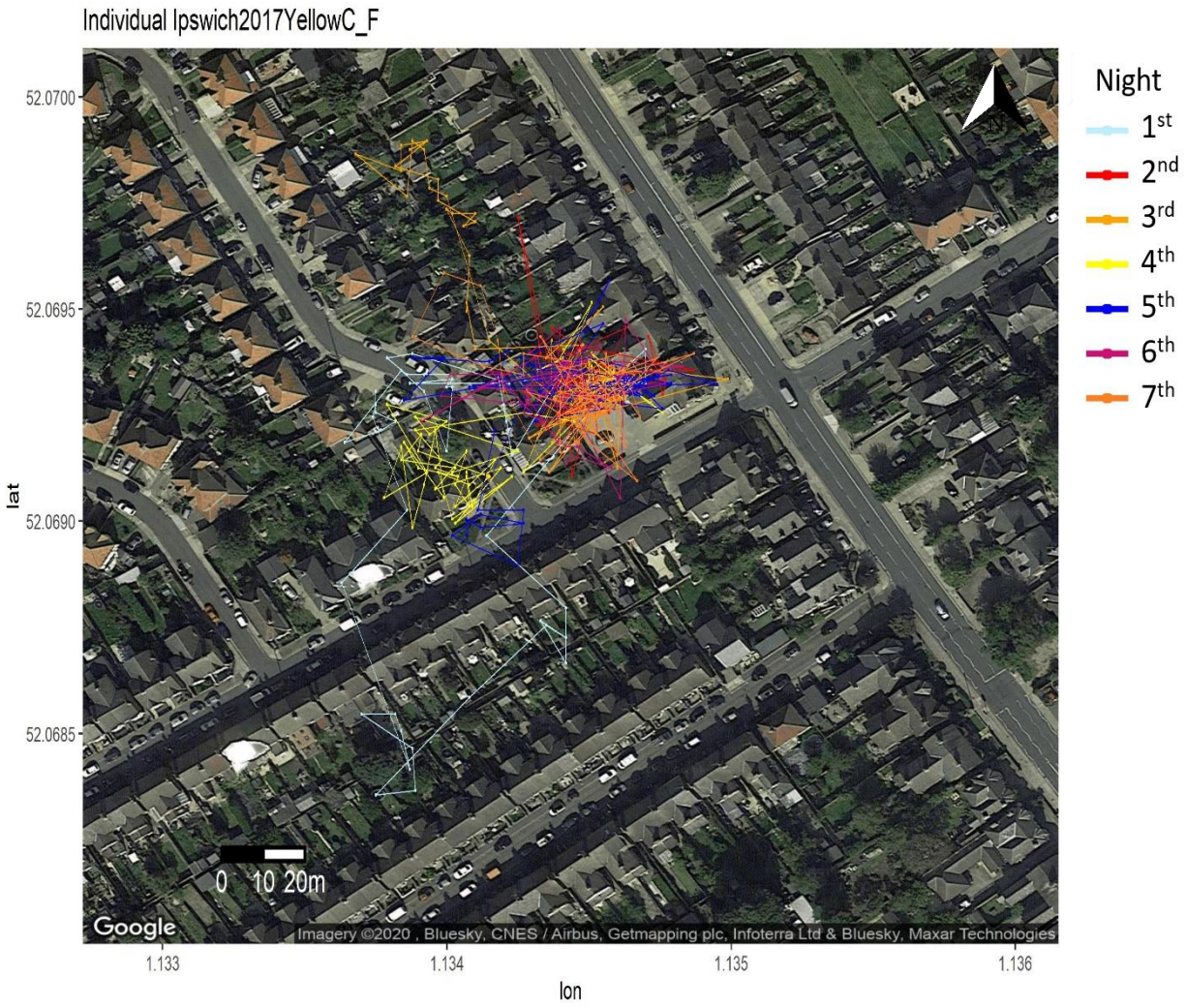



Figure D-40. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Ipswich West 2017 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).


Figure D-41. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Ipswich East 2018 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).


Figure D-42. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Ipswich East 2018 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

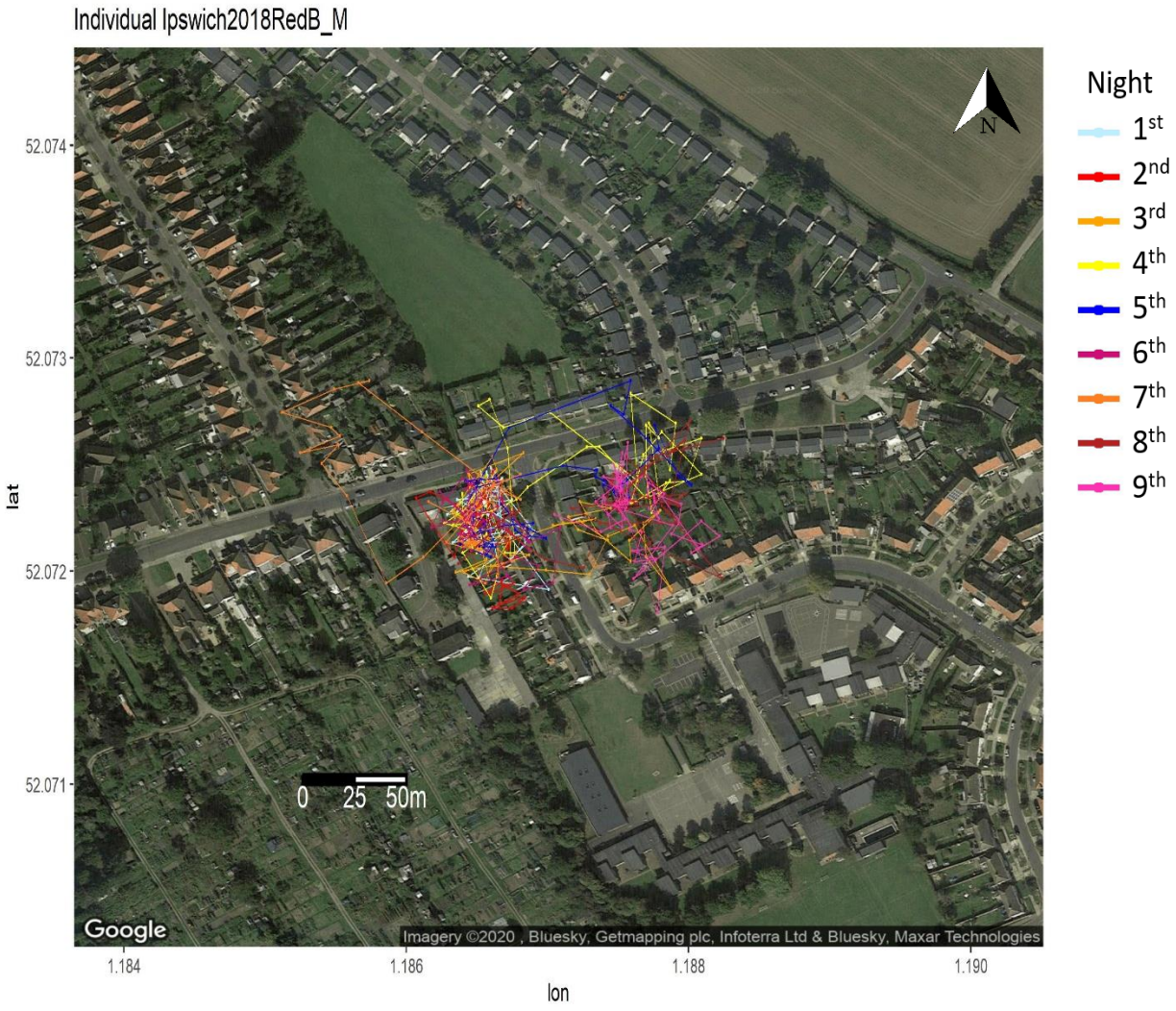



Figure D-43. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Ipswich East 2018 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

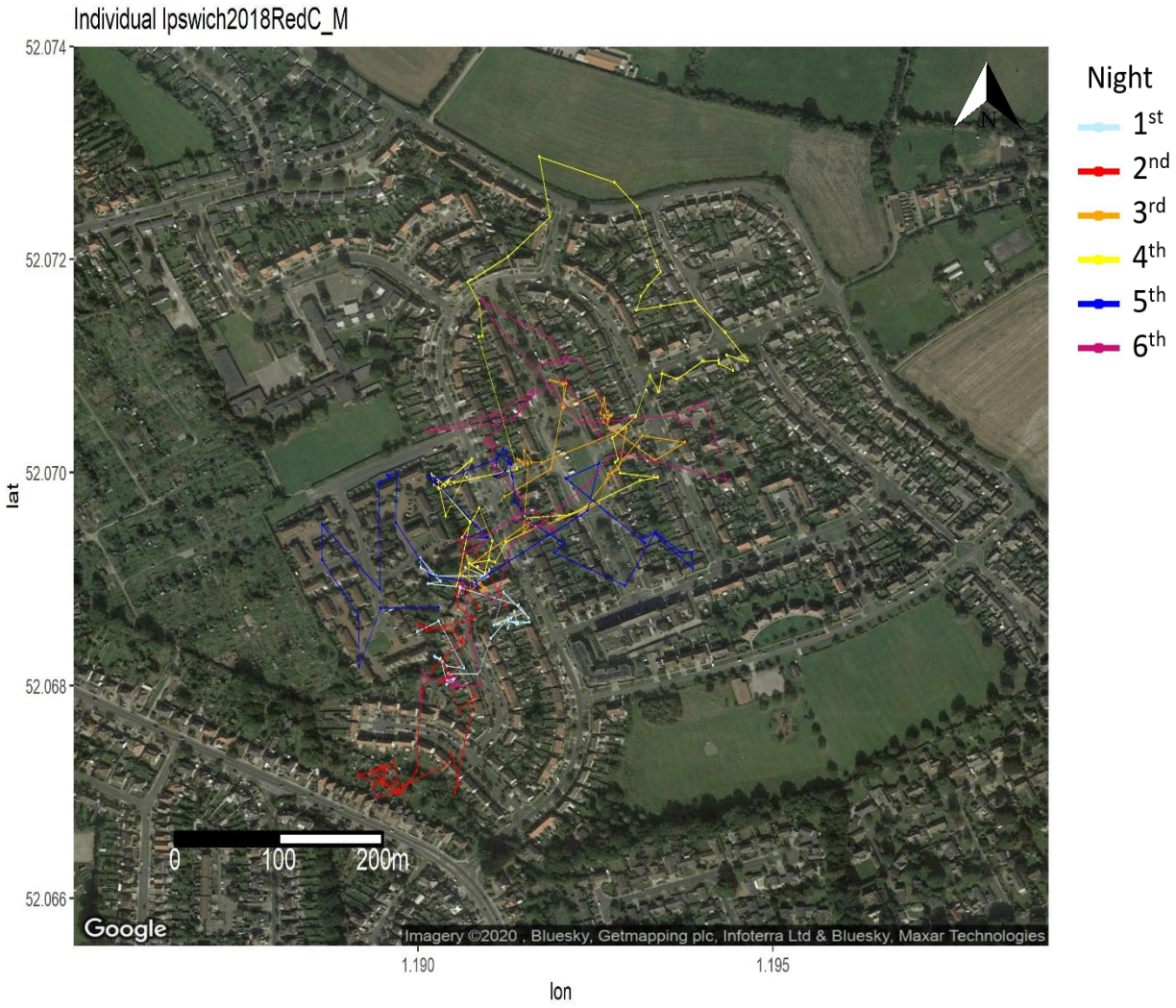



Figure D-44. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Ipswich East 2018 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

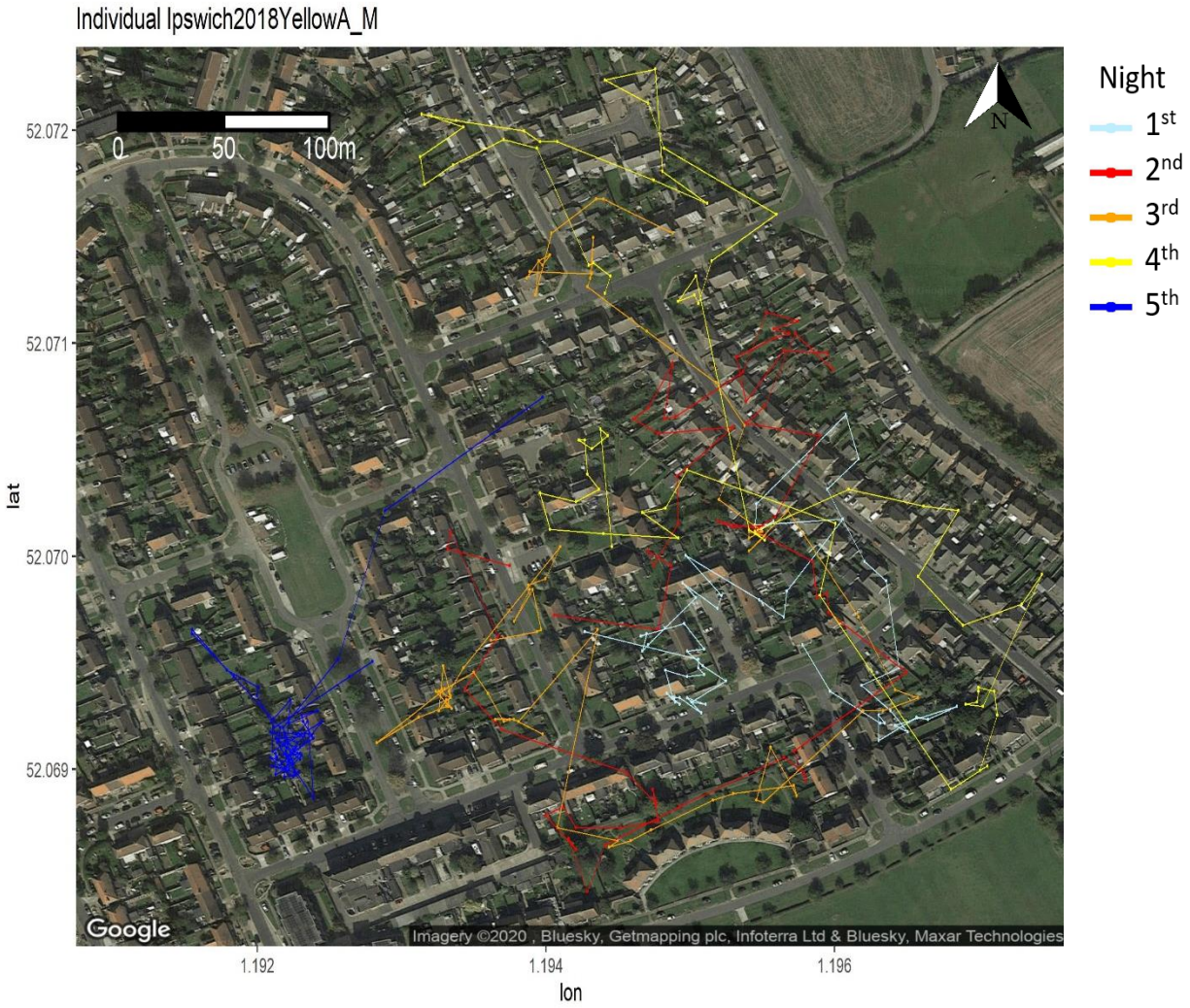



Figure D-45. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Ipswich East 2018 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

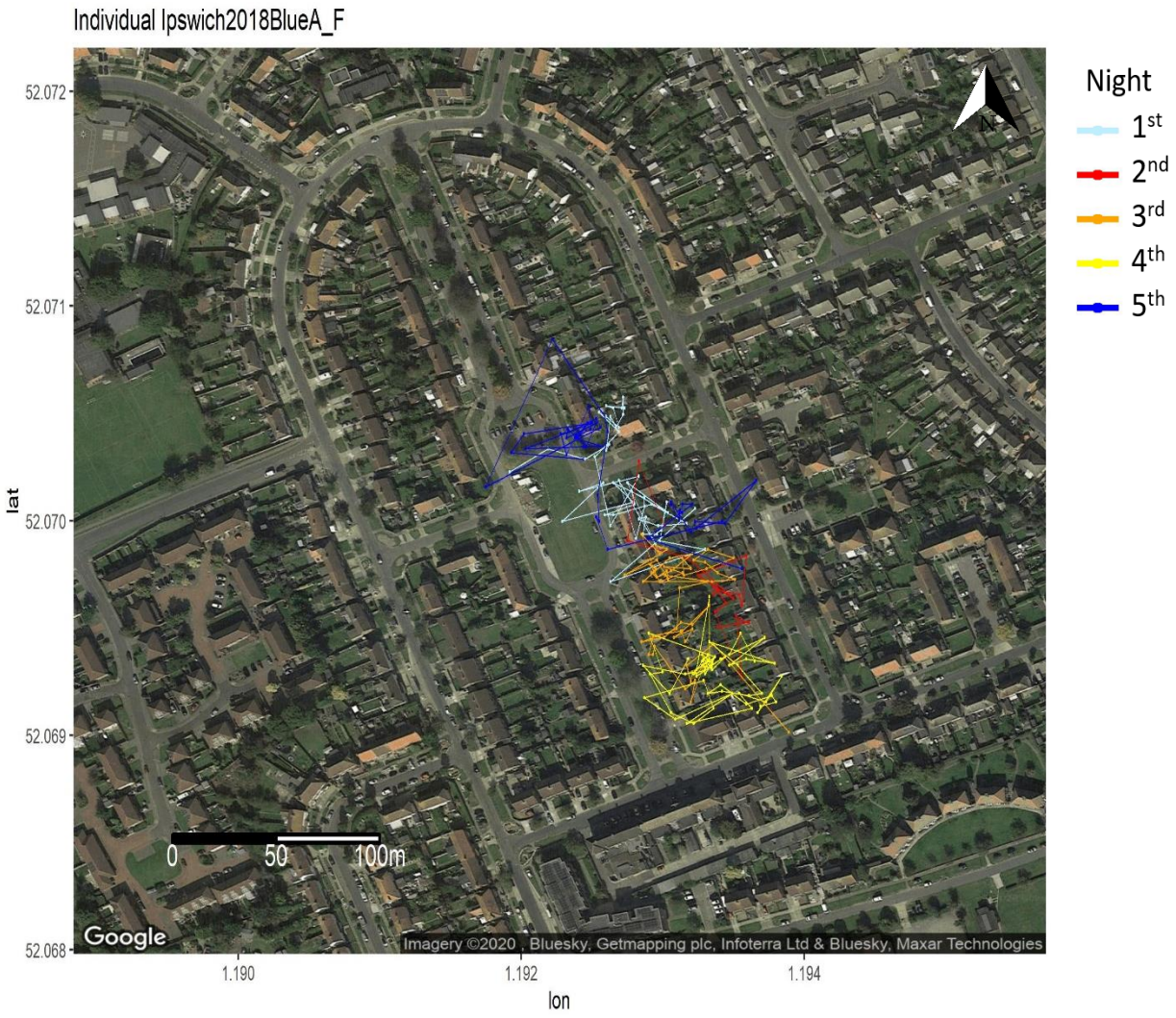



Figure D-46. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Ipswich East 2018 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

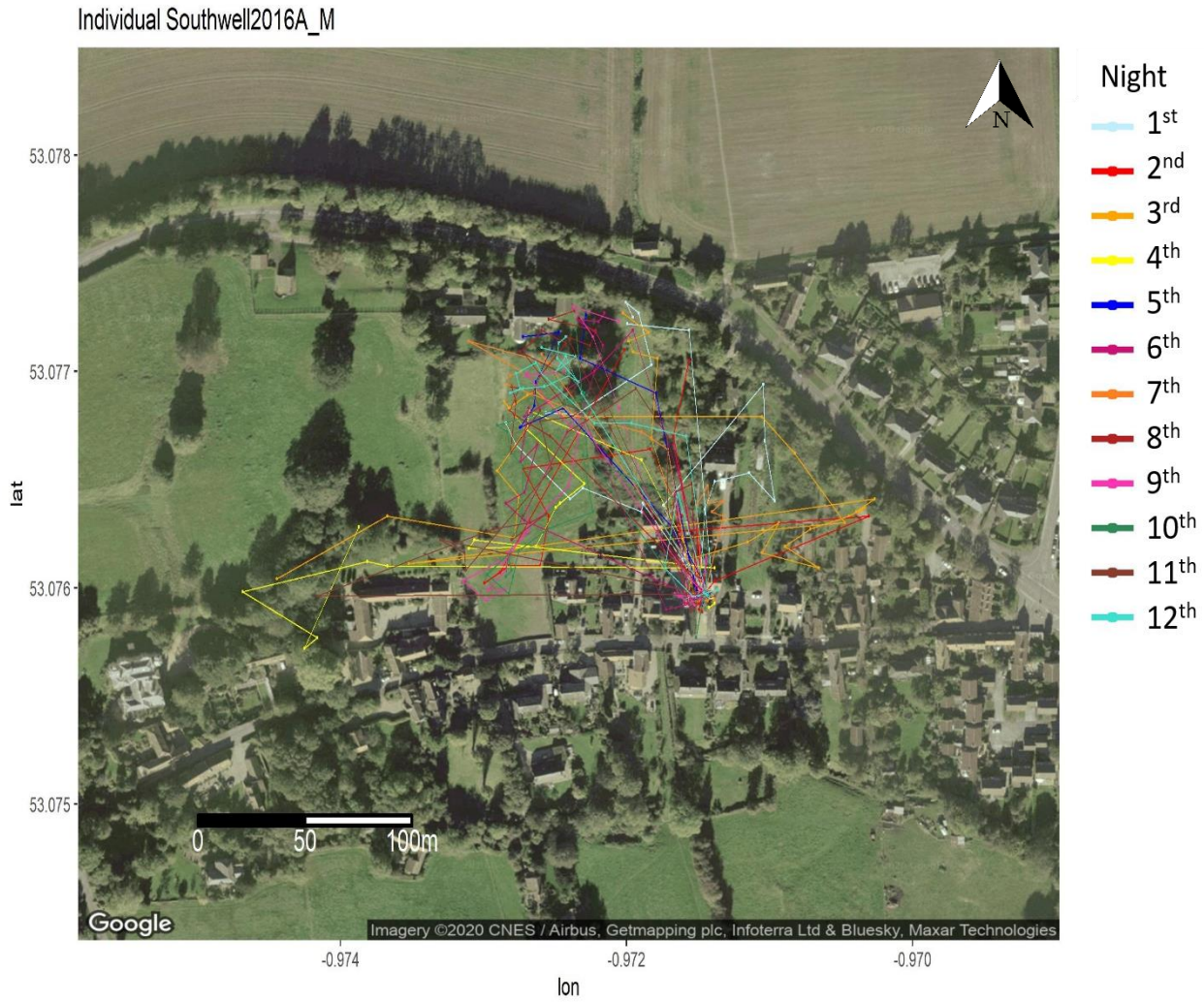



Figure D-47. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Southwell 2016 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

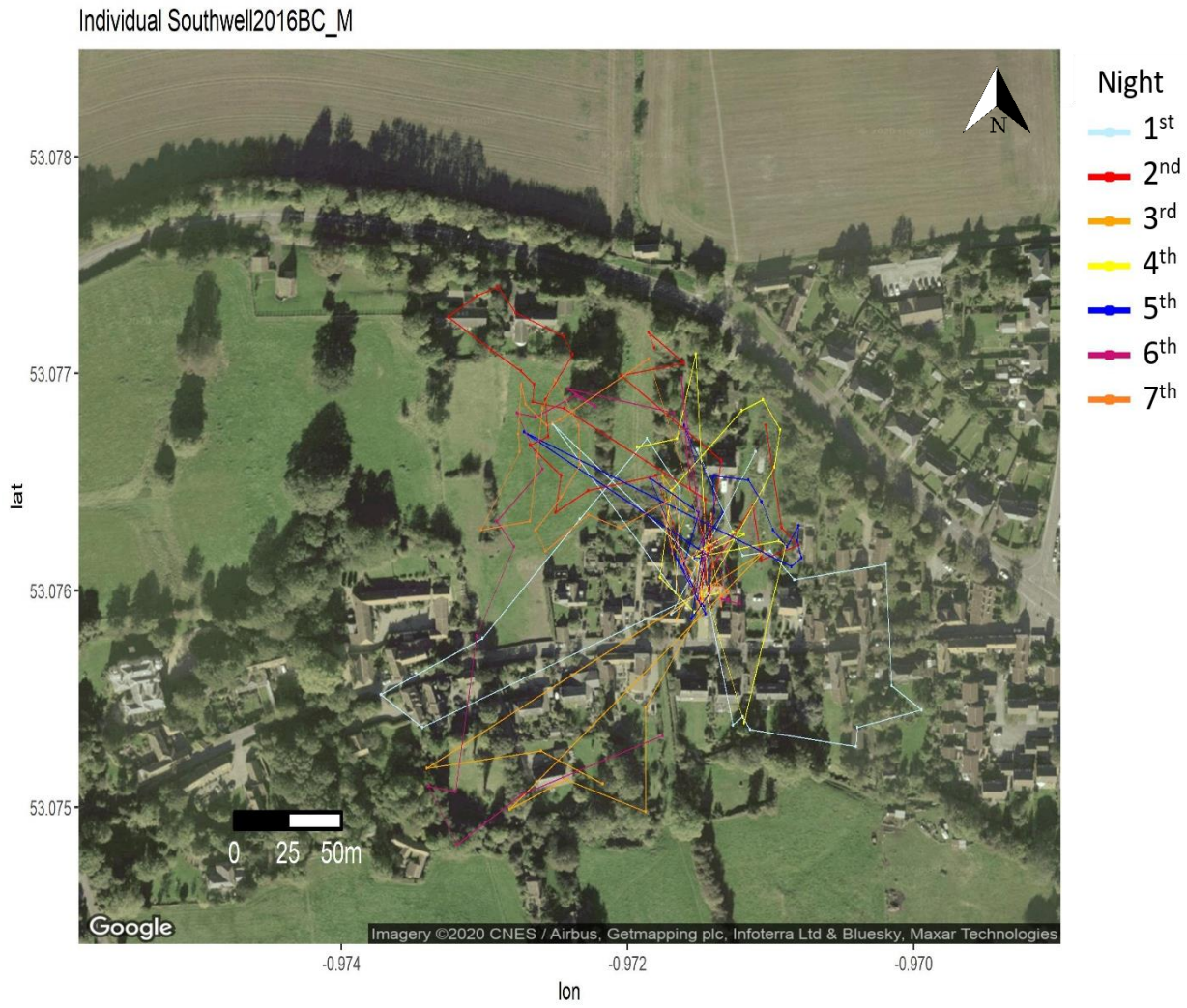



Figure D-48. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Southwell 2016 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

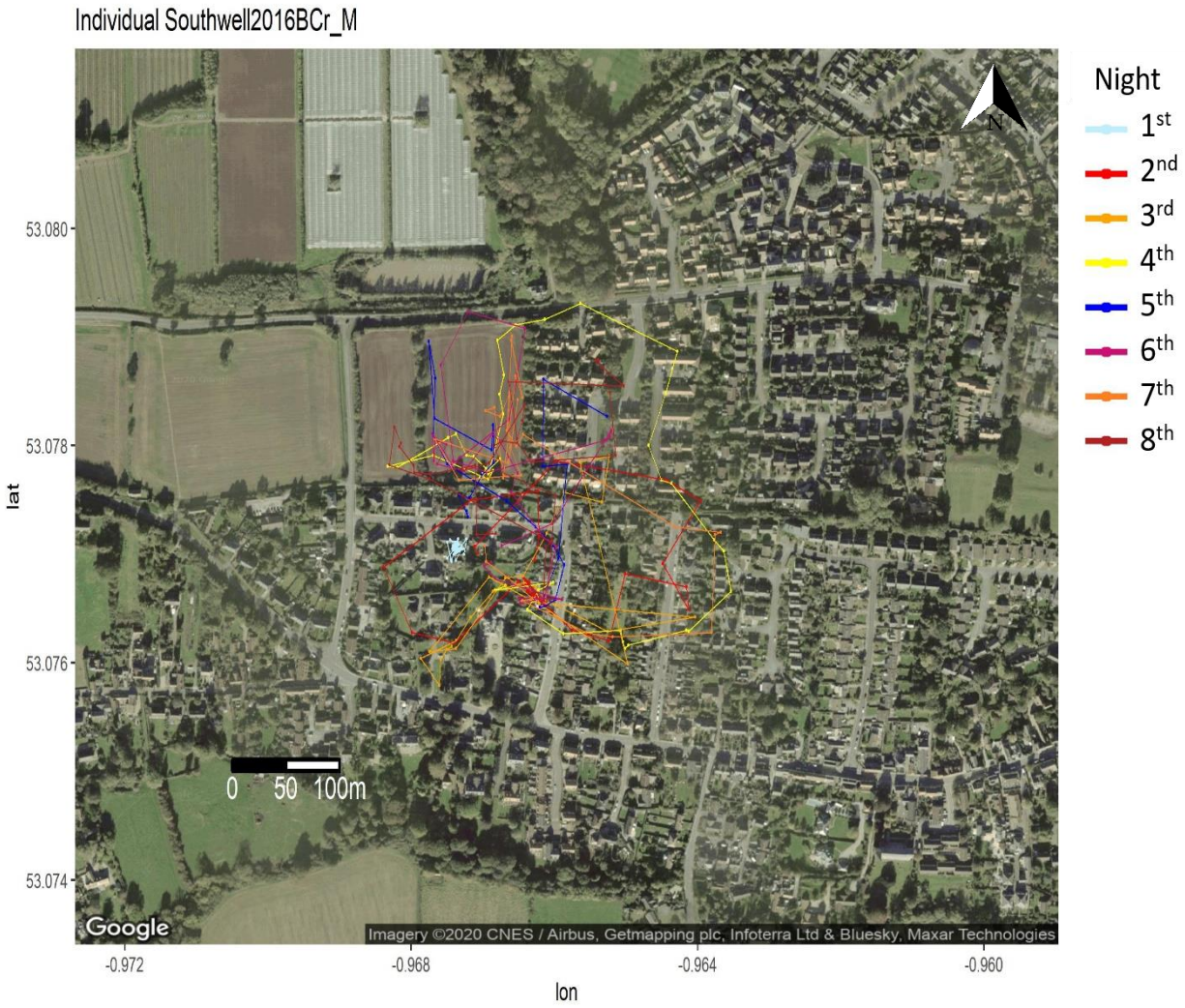



Figure D-49. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Southwell 2016 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

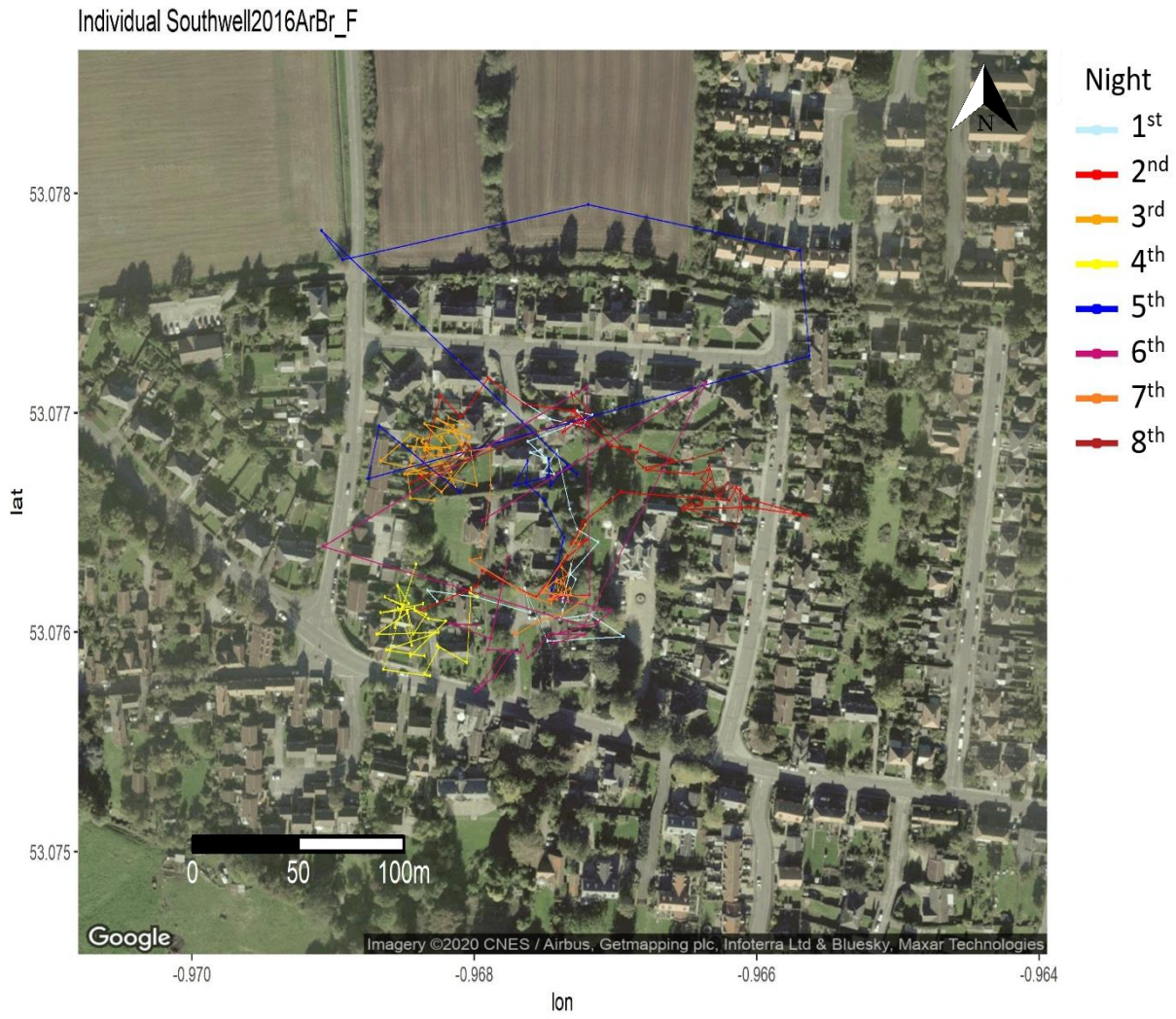



Figure D-50. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Southwell 2016 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

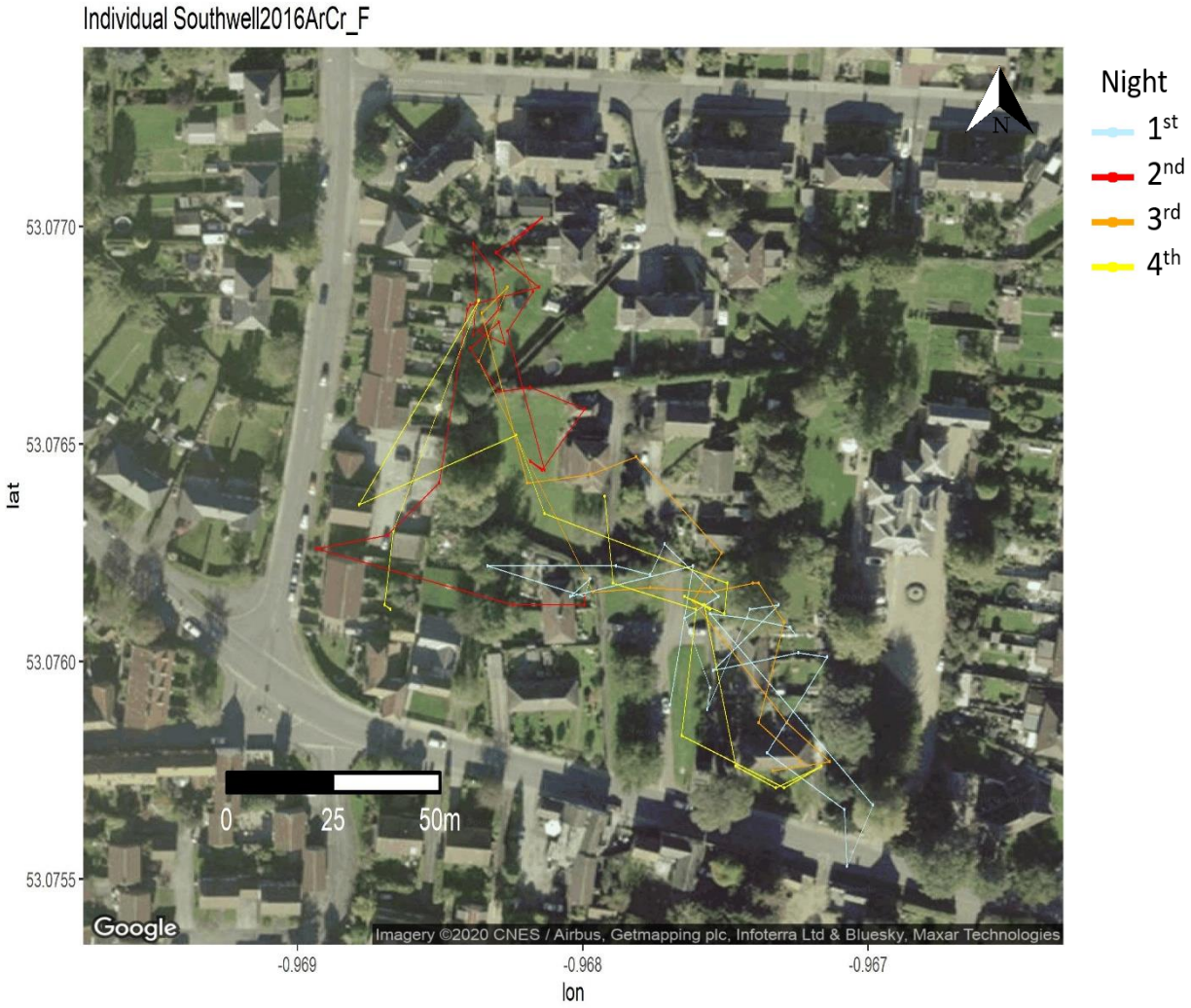



Figure D-51. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Southwell 2016 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

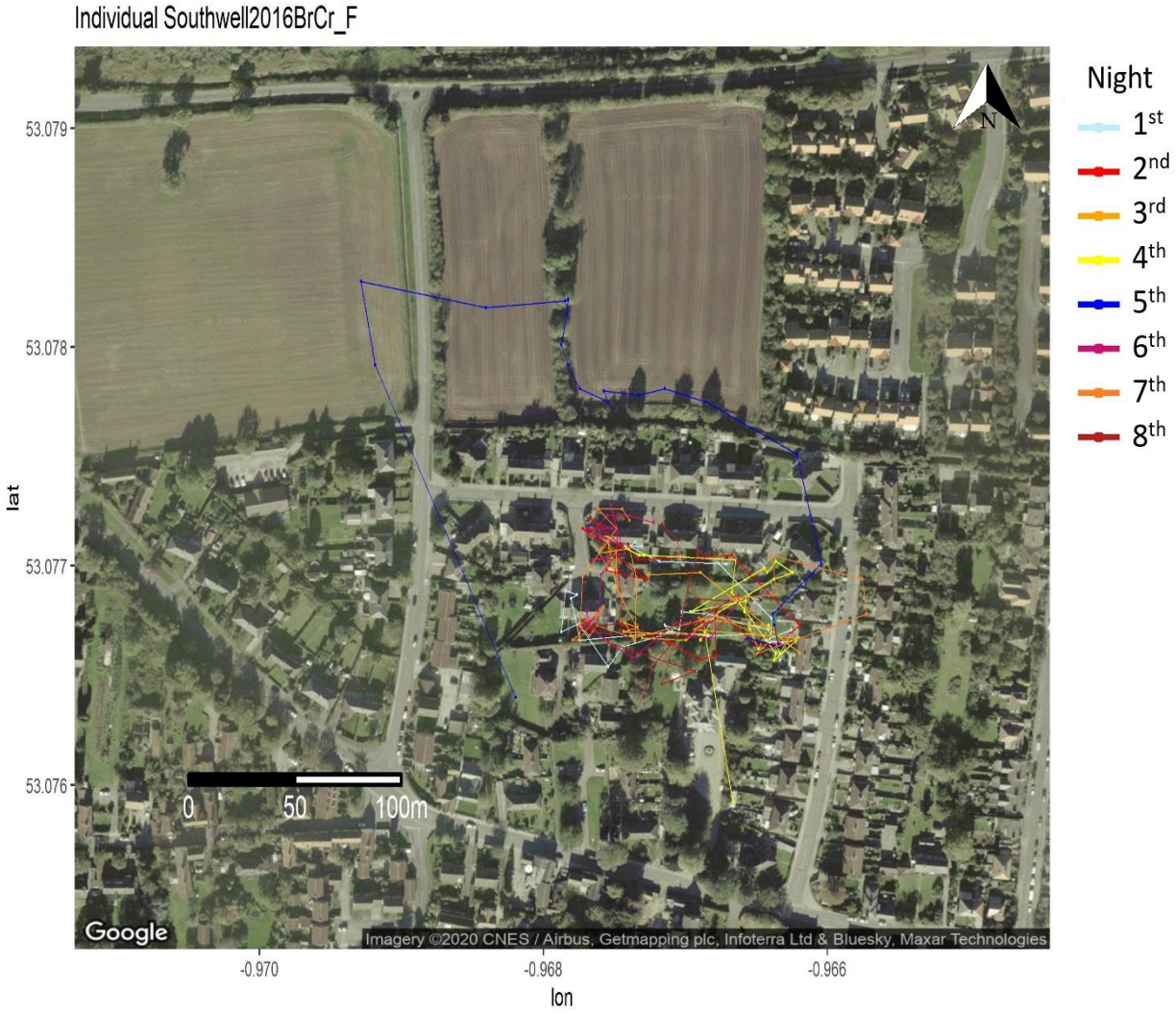



Figure D-52. Movement data of a male urban West European hedgehog (*Erinaceus europaeus*) at Southwell 2016 (UK). Different colours represent different nights; points represent locations recorded approximately every five minutes; lines connect consecutive locations. Maps produced with ggmap R package (Kahle and Wickham, 2013).

**Appendix E** West European hedgehogs (*Erinaceus europaeus*) radio-tracked in urban and rural landscapes between 2016 and 2019 in England. The table includes the sex of the individuals, weight (g) during the tracking period, number of days the GPS tags were on the individuals and the total number of GPS fixes recorded. Negative weight variation indicates that the individual lost weight during the time it had the GPS tag attached. Speed is given in metres per second, and nightly distances in metres. g=grams, SD= Standard Deviation.

| Landscape | Site | Hedgehog ID | Sex | Initial weigth (g) | Final weigth (g) | Weight variation (g) | No of days tracked | Tracking period | | Total number of GPS fixes | Speed (m/s) | | Nighly distance travelled (m) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | Start | End | | Mean | SD | Mean | SD |
| Rural | Bishop Burton 2019 | BlueA_M | M | 978 | | | 9 | 17/08/19 | 26/08/19 | 478 | 0.061 | 0.023 | 1249 | 801 |
| | | BlueB_F | F | 1032 | 920 | -112 | 9 | 17/08/19 | 26/08/19 | 521 | 0.050 | 0.003 | 1226 | 88 |
| | | BlueC_M | M | 933 | 958 | 25 | 10 | 16/08/19 | 26/08/19 | 700 | 0.057 | 0.007 | 1436 | 238 |
| | | BlueD_F | F | 957 | 1016 | 59 | 10 | 16/08/19 | 26/08/19 | 709 | 0.054 | 0.007 | 1349 | 184 |
| | | BlueE_F | F | 815 | 801 | -14 | 9 | 17/08/19 | 26/08/19 | 481 | 0.047 | 0.009 | 1129 | 172 |
| | | BlueG_M | M | 967 | 1063 | 96 | 9 | 17/08/19 | 26/08/19 | 311 | 0.050 | 0.011 | 1092 | 335 |
| | Brackenhurst 2017 | BlackDD_F | F | 766 | 867 | 101 | 10 | 14/09/17 | 24/09/17 | 888 | 0.040 | 0.006 | 1168 | 264 |
| | | BlackEE_F | F | 1009 | 965 | -44 | 9 | 14/09/17 | 23/09/17 | 798 | 0.054 | 0.005 | 1624 | 262 |
| | | BlackHH_F | F | 802 | 811 | 9 | 7 | 16/09/17 | 23/09/17 | 702 | 0.053 | 0.007 | 1671 | 187 |
| | | BlueCC_M | M | 1030 | 1047 | 17 | 9 | 15/09/17 | 24/09/17 | 792 | 0.050 | 0.004 | 1382 | 133 |
| | Brackenhurst 2018 | BlackDD_F | F | 704 | 796 | 92 | 9 | 25/04/18 | 04/05/18 | 653 | 0.046 | 0.008 | 1143 | 240 |
| | | BlackEE_F | F | 947 | 997 | 50 | 13 | 19/04/18 | 02/05/18 | 932 | 0.040 | 0.008 | 907 | 286 |
| | | BlueAA_F | F | 733 | 793 | 60 | 9 | 25/04/18 | 04/05/18 | 518 | 0.037 | 0.007 | 813 | 127 |
| | | BlueCC_M | M | 1060 | 968 | -92 | 13 | 19/04/18 | 02/05/18 | 1020 | 0.066 | 0.009 | 1678 | 293 |
| | | YellowAA_M | M | 774 | 772 | -2 | 8 | 26/04/18 | 04/05/18 | 570 | 0.084 | 0.022 | 2083 | 648 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Hartpury 2017 | BH_M | M | 857 | 836 | -21 | 9 | 21/06/17 | 30/06/17 | 249 | 0.100 | 0.032 | 1952 | 646 |
| | | RA_M | M | 689 | 660 | -29 | 9 | 21/06/17 | 30/06/17 | 501 | 0.059 | 0.011 | 1081 | 319 |
| | | RB_F | F | 775 | 804 | 29 | 9 | 22/06/17 | 01/07/17 | 561 | 0.050 | 0.012 | 1010 | 219 |
| | | RH_F | F | 919 | 1046 | 127 | 4 | 27/06/17 | 01/07/17 | 141 | 0.051 | 0.008 | 718 | 176 |
| | Riseholme 2019 | BlueA_M | M | 1038 | 1100 | 62 | 11 | 09/09/19 | 20/09/19 | 823 | 0.079 | 0.011 | 2247 | 389 |
| | | BlueB_F | F | 859 | 814 | -45 | 11 | 09/09/19 | 20/09/19 | 868 | 0.055 | 0.009 | 1731 | 308 |
| | | BlueC_F | F | 882 | 957 | 75 | 11 | 09/09/19 | 20/09/19 | 790 | 0.052 | 0.006 | 1419 | 192 |
| | Sutton Bonington 2018 | YellowA_F | F | 1098 | 899 | -199 | 10 | 04/07/18 | 14/07/18 | 233 | 0.062 | 0.016 | 832 | 268 |
| Urban | Brighton 2018 | Blue_E_F | F | 778 | 777 | -1 | 10 | 10/05/18 | 20/05/18 | 570 | 0.031 | 0.005 | 659 | 132 |
| | | BlueA_M | M | 996 | 979 | -17 | 10 | 10/05/18 | 20/05/18 | 565 | 0.070 | 0.011 | 1477 | 302 |
| | | BlueC_M | M | 802 | | | 13 | 08/05/18 | 21/05/18 | 777 | 0.056 | 0.014 | 1233 | 340 |
| | | RedC_F | F | 798 | 834 | 36 | 8 | 11/05/18 | 19/05/18 | 342 | 0.029 | 0.007 | 525 | 136 |
| | | RedD_F | F | 1112 | 1236 | 124 | 7 | 11/05/18 | 18/05/18 | 382 | 0.030 | 0.005 | 621 | 128 |
| | | YellowA_M | M | 690 | 762 | 72 | 11 | 08/05/18 | 19/05/18 | 613 | 0.059 | 0.018 | 1236 | 353 |
| | | YellowC_M | M | 747 | 711 | -36 | 9 | 11/05/18 | 20/05/18 | 497 | 0.053 | 0.008 | 1074 | 222 |
| | Brighton 2019 | BlackA_M | M | 1071 | 1088 | 17 | 11 | 20/06/19 | 01/07/19 | 203 | 0.045 | 0.010 | 620 | 165 |
| | | BlackC_F | F | 712 | 800 | 88 | 10 | 22/06/19 | 02/07/19 | 388 | 0.039 | 0.006 | 658 | 121 |
| | | BlackD_M | M | 931 | 1083 | 152 | 14 | 22/06/19 | 06/07/19 | 483 | 0.052 | 0.011 | 861 | 172 |
| | | BlueA_F | F | 878 | 929 | 51 | 8 | 17/06/19 | 25/06/19 | 368 | 0.046 | 0.008 | 837 | 168 |
| | | RedA_M | M | 1214 | 1131 | -83 | 9 | 27/06/19 | 06/07/19 | 233 | 0.074 | 0.015 | 1217 | 357 |
| | | RedC_F | F | 769 | 717 | -52 | 9 | 30/06/19 | 09/07/19 | 250 | 0.092 | 0.026 | 1309 | 435 |
| | Ipswich 2017 | BlueF_F | F | 877 | | | 6 | 20/04/17 | 26/04/17 | 285 | 0.044 | 0.009 | 779 | 62 |
| | | RedC_M | M | 942 | 896 | -46 | 5 | 21/04/17 | 26/04/17 | 292 | 0.061 | 0.009 | 1332 | 305 |
| | | RedH_F | F | 710 | 720 | 10 | 9 | 22/04/17 | 01/05/17 | 287 | 0.042 | 0.004 | 763 | 181 |
| | | YellowC_F | F | 707 | 751 | 44 | 7 | 19/04/17 | 26/04/17 | 451 | 0.034 | 0.003 | 758 | 91 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Ipswich 2018 | Blue_A_M | M | 1006 | | | 5 | 07/04/18 | 12/04/18 | 55 | 0.112 | | 2501 | |
| | | Blue_D_M | M | 728 | 687 | -41 | 4 | 12/04/18 | 16/04/18 | 256 | 0.057 | 0.008 | 1285 | 134 |
| | | BlueA_F | F | 623 | 630 | 7 | 5 | 10/04/18 | 15/04/18 | 239 | 0.042 | 0.006 | 716 | 217 |
| | | RedB_M | M | 725 | | | 9 | 04/04/18 | 13/04/18 | 500 | 0.041 | 0.007 | 801 | 175 |
| | | RedC_M | M | 735 | 770 | 35 | 6 | 08/04/18 | 14/04/18 | 304 | 0.071 | 0.018 | 1437 | 439 |
| | | YellowA_M | M | 941 | 937 | -4 | 5 | 11/04/18 | 16/04/18 | 340 | 0.059 | 0.013 | 1348 | 324 |
| | Southwell 2016 | A_M | M | 655 | 858 | 203 | 14 | 15/06/16 | 29/06/16 | 329 | 0.050 | 0.015 | 731 | 208 |
| | | ArBr_F | F | 871 | 771 | -100 | 11 | 02/06/16 | 13/06/16 | 252 | 0.041 | 0.018 | 602 | 222 |
| | | ArCr_F | F | 765 | 867 | 102 | 10 | 02/06/16 | 12/06/16 | 94 | 0.032 | 0.005 | 418 | 43 |
| | | BC_M | M | 784 | 990 | 206 | 9 | 16/06/16 | 25/06/16 | 186 | 0.057 | 0.012 | 859 | 148 |
| | | BCr_M | M | 866 | 909 | 43 | 11 | 11/06/16 | 22/06/16 | 261 | 0.076 | 0.025 | 1107 | 366 |
| | | BrCr_F | F | 946 | 856 | -90 | 11 | 02/06/16 | 13/06/16 | 200 | 0.033 | 0.009 | 427 | 88 |

**Appendix F** Hidden Markov Models (HMM) showing which covariates best explain the movement states and the transition probabilities of hedgehogs. AIC= Akaike's Information Criterion, $\Delta_i$ = delta AIC, $\omega$= AIC weighting.

| Model | Model | AIC | $\Delta_i$ | w |
|---|---|---|---|---|
| M21 | Sex + Habitat + Distance to buildings + Distance to gardens | 199499.7 | 0 | 0.602 |
| M29 | Sex + Habitat + Distance to buildings + Distance to gardens + Distance to roads | 199501.6 | 2 | 0.227 |
| M26 | Sex + Habitat + Distance to gardens | 199502.4 | 3 | 0.153 |
| M25 | Sex + Habitat + Distance to buildings | 199507.3 | 8 | 0.014 |
| M22 | Sex + Habitat + Distance to buildings + Distance to roads | 199509.4 | 10 | 0.005 |
| M23 | Sex + Distance to gardens + Distance to buildings | 199517.2 | 18 | 0 |
| M13 | Sex + Distance to gardens | 199519.7 | 20 | 0 |
| M14 | Sex + Habitat | 199521.5 | 22 | 0 |
| M27 | Sex + Habitat + Distance to roads | 199522.4 | 23 | 0 |
| M24 | Sex + Distance to gardens + Distance to roads | 199523.5 | 24 | 0 |
| M12 | Sex + Distance to buildings | 199534.3 | 35 | 0 |
| M28 | Sex + Distance to roads + Distance to buildings | 199537.1 | 37 | 0 |
| M15 | Sex + Distance to roads | 199545.2 | 46 | 0 |
| M02 | Sex | 199546.3 | 47 | 0 |
| M08 | Habitat + Distance to garden | 199696.5 | 197 | 0 |
| M19 | Habitat + Distance to gardens + Distance to roads | 199698.1 | 198 | 0 |
| M18 | Habitat + Distance to gardens + Distance to buildings | 199698.7 | 199 | 0 |
| M07 | Habitat + Distance to buildings | 199706.5 | 207 | 0 |
| M20 | Habitat + Distance to roads + Distance to buildings | 199708.2 | 209 | 0 |
| M05 | Distance to gardens | 199710.5 | 211 | 0 |
| M16 | Distance to buildings + Distance to gardens | 199712.9 | 213 | 0 |
| M11 | Distance to roads + Distance to gardens | 199713.4 | 214 | 0 |
| M03 | Habitat + Distance to roads | 199714.8 | 215 | 0 |
| M09 | Habitat | 199715.4 | 216 | 0 |
| M06 | Distance to gardens + Distance to roads + Distance to buildings | 199716.1 | 216 | 0 |
| M17 | Distance to buildings | 199716.3 | 217 | 0 |
| M10 | Distance to roads + Distance to buildings | 199718.1 | 218 | 0 |
| M04 | Distance to Roads | 199721.0 | 221 | 0 |
| M01 | Null | 199722.2 | 222 | 0 |